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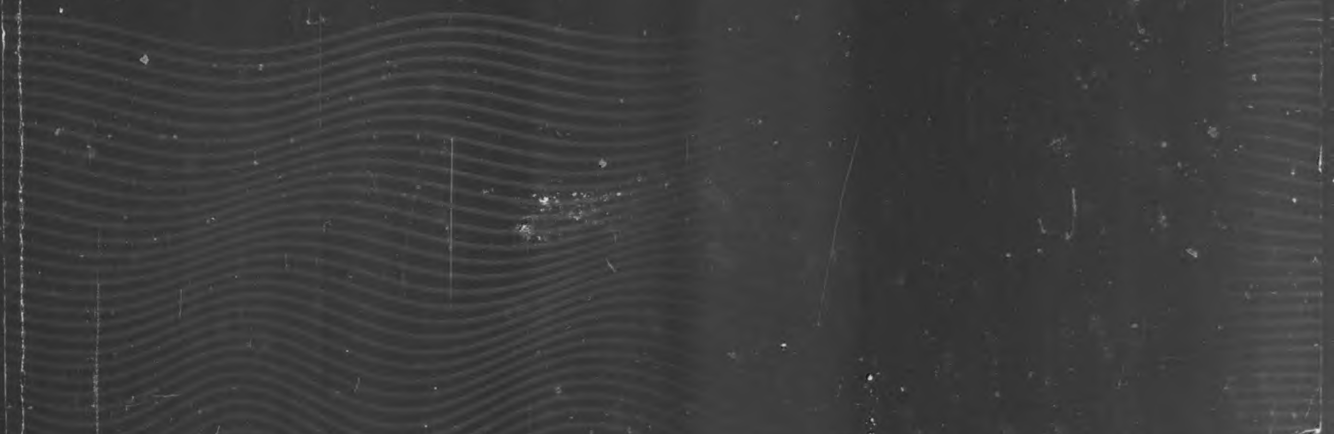

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Lake Use by Wild Anadromous Atlantic Salmon, *Salmo salar*, as an Index of Subsequent Adult Abundance

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Ryan, P. M. 1986. Lake use by wild anadromous Atlantic salmon, *Salmo salar*, as an index of subsequent adult abundance. Can. J. Fish. Aquat. Sci. 43: 2–11.

Atlantic salmon, *Salmo salar*, were censused each spring and fall for 5 or 6 yr in two lakes at the headwaters of the Gander River, Newfoundland. Density, biomass, and age varied seasonally and annually, ranging from 5.2 to 78.7 $\text{fish}\cdot\text{ha}^{-1}$, 0.2 to 3.4 $\text{kg}\cdot\text{ha}^{-1}$, and 1 to 7 yr, respectively. Seasonal changes in age composition were used to calculate net numbers and ages of fish moving into and out of the lakes. Population sizes typically increased from fall to spring as young fish moved into the lakes from downstream spawning areas and decreased from spring to fall as older fish moved downstream. The calculated net number of spring to fall emigrants over 6 yr was positively correlated ($r = 0.835$) with adult abundance (catch per unit effort) in the recreational fishery 1 yr later. The varying modal age of these emigrants was identical to the modal freshwater age of returning adults in each of four comparable years. Censusing of young Atlantic salmon in standing waters can be used to monitor smolt production and assist in prediction of the subsequent abundance of sea-run adults.

On a dénombré les saumons de l'Atlantique (*Salmo salar*) chaque printemps et chaque automne pendant 5 ou 6 ans dans deux lacs situés à la source de la rivière Gander, à Terre-Neuve. La densité, la biomasse et l'âge ont fluctué suivant la saison et l'année, ces paramètres variant respectivement de 5,2 à 78,7 poissons/ha, de 0,2 à 3,4 kg/ha et de 1 à 7 ans. On s'est servi des changements saisonniers de la composition par âge pour calculer le nombre net et l'âge des poissons qui pénètrent dans les lacs et en sortent. La taille des populations a augmenté de façon caractéristique de l'automne au printemps, lorsque les jeunes poissons ont pénétré dans les lacs, venant des aires de fraye situées en aval, et a diminué du printemps à l'automne, période au cours de laquelle les poissons plus âgés se sont dirigés vers l'aval. On a trouvé une corrélation positive ($r = 0,835$) entre le nombre net des émigrants (du printemps à l'automne) calculé sur une période de 6 ans et l'abondance des adultes (prises par unité d'effort) capturés par les pêcheurs sportifs 1 an plus tard. L'âge modal variable de ces émigrants était identique à l'âge modal en eau douce des adultes qui sont revenus dans chacune des quatre années comparables. Le recensement de jeunes saumons de l'Atlantique dans les eaux stagnantes peut servir à surveiller la production de saumoneaux et aider à prédire l'abondance ultérieure des adultes anadromes.

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After hatching in stream spawning areas, young Atlantic salmon, *Salmo salar*, may ascend or descend river systems and inhabit lakes as well as streams for varying periods (Huntsman 1945). A year or more after the seaward migration of smolts, returning adults are harvested in commercial and recreational fisheries or escape to rivers to spawn (Scott and Crossman 1973). For management purposes, juvenile abundance is monitored with fish counting fences (Chadwick et al. 1978) and fishways (O'Connell et al. 1983) as the smolts move to sea, or by population estimates in stream habitats (Marshall 1983). Smolt production is used to predict the subsequent abundance of adults (Chadwick et al. 1978; Ruggles 1980; Chadwick 1982a).

In rivers where the installation of counting facilities is not practical due to factors such as frequent flooding or high costs, estimation of smolt production is difficult because of the variety of habitats occupied by young salmon and the uncertainties associated with the selection of representative habitat types (Marshall 1983). Lakes are a representative habitat type used by anadromous Atlantic salmon in Newfoundland (Pepper 1985) and, to a lesser extent, elsewhere (Rimmer et al. 1983). 1976; Dalley et al. 1983; Ryan 1984a; Chadwick and Green There is evidence that the use of lake habitat by young salmon depends, to a large extent, on its availability and tends to increase at higher stock densities (Pepper 1976; Rimmer et al. 1983; Gibson and Dickson 1984; Chadwick and Green 1985). However, the importance of lakes to salmon production is not clear due to the scarcity of quantitative information about lake use by salmon in areas where lakes are a dominant feature of river systems. In insular Newfoundland, over 10% of the land mass is covered by standing waters larger than 0.4 ha (Whelan and Wiseman 1975) and there is evidence that, in at least one river system, the majority of smolt production occurs in lacustrine habitat (Chadwick and Green 1985).

This report documents the long-term seasonal and annual variations in density, biomass, and age composition of the freshwater forms of an anadromous Atlantic salmon stock in two small lakes at the headwaters of one of Newfoundland's largest river systems. Changes in age composition were used to calculate the net numbers and ages of fish moving into and out of the lakes on a seasonal basis. Emigrations from the lakes over the spring to fall period are shown to be indicative of smolt production and the subsequent abundance of sea-run adults.

Methods

Study Area

The physical and chemical characteristics of Headwater Pond (48°16′15″N, 55°29′39″W) and Spruce Pond (48°19′40″N, 55°28′24″W) have been described by Ryan and Wakeham (1984). In summary, they are dilute (mean conductance 35 $\mu S \cdot cm^{-1}$), brown-water lakes within the Department of Fisheries and Oceans' Experimental Ponds Area at the headwaters of the Gander River system. The Gander River has insular Newfoundland's largest river basin area that is accessible to anadromous salmon (Murray and Harmon 1969). Headwater Pond (76.1 ha, maximum depth = 3.3 m, mean depth = 1.1 m) has one inlet, and an outlet draining 3.5 km north to Spruce Pond (36.5 ha, maximum depth = 2.1 m, mean depth = 1.0 m). Spruce Pond has an additional minor inlet, and an outlet draining about 155 km northeast to the Atlantic Ocean. In addition to Atlantic salmon, both lakes are populated by brook trout (*Salvelinus fontinalis*) (Cone and Ryan 1984; Ryan 1984a), American eel (*Anguilla rostrata*), and threespine stickleback (*Gasterosteus aculeatus*) (Ryan 1984b). The Atlantic salmon are part of a sea-run stock, and those considered in the present study are the immature and precociously mature forms which had not left freshwaters. Negligible amounts of suitable spawning area for Atlantic salmon occur near the study lakes, and the closest major concentration of spawning substrate is about 12 km downstream of Spruce Pond (Traverse 1972; Ryan and Wakeham 1984).

Population Structure

Salmon were censused each spring and fall by Schnabel's multiple mark−recapture method (Ricker 1975) starting in 1978 in Spruce Pond and 1979 in Headwater Pond. Fish were captured in 13- and 19-mm stretched mesh fyke nets, measured for fork length (millimetres), marked with fin clips or fin holes, and released as described in Ryan (1984a). The marking rate, estimated from the number of marked fish as a percentage of each population estimate, averaged 45% with a range of 21−70%. The recapture rate, estimated from the number of marked fish as a percentage of the last day's catch in each estimate, averaged 41% with a range of 11−79%. Weights (grams) and scale samples were obtained from a subsample of fish selected approximately at random near the beginning of each census with subsequent emphasis on less frequently encountered length intervals. Ages were assigned to the fish as described by Tesch (1971). Ages were considered reliable on the basis of correspondence among back-calculated lengths, empirical lengths of fish assigned to given age-groups, and length and age increments of fish recognizable as members of discrete year-classes (see Tesch 1971; Nickerson et al. 1980; Ryan et al. 1981). The age composition of fish in each lake during each population estimate was calculated from the ages and lengths of fish in the subsample, the lengths of captured and released fish, the Schnabel population estimate, and their relative proportions using age−length keys (Ricker 1975). The weight of fish in each lake during each census was calculated by summing the products of the mean weight of individuals in each age-group in the aged subsample and the calculated number in each age-group in the lake.

Population Dynamics

The net number of fish in each age-group migrating into or out of the lakes between population estimates was calculated as the difference between the number of fish in each age-group present during a given census and those present during the subsequent census. For the purpose of calculating fall to spring changes, fish caught in the spring were considered to be members of age-groups 1 yr younger. For example, fish first encountered in the lakes in the spring as members of age-group 1 were calculated to have entered the lakes between the spring and the preceding fall as members of age-group 0. The hypothesis that the calculated number of lake emigrants each spring to fall was an ocean-bound smolt run was tested by comparing the calculated number and age composition of fish emigrating out of the lakes from spring to fall to the relative abundance and age composition of adult one-sea-winter fish (grilse) in the Gander River recreational angling fishery 1 yr later. Total recreational catch has been shown to be an index of total adult returns in eight Newfoundland rivers where adult counting facilities were present, including a small tributary of the Gander River (Chadwick 1982b). In the present study, I used observed catch per unit effort as the measure of adult abundance (Ricker 1975) to compensate for varying effort during the short time series. Average river water level in each year of adult capture was calculated to compensate for increases in catchability associated with decreased discharge (Chadwick 1982a, 1982b). Values of −1, 0, and +1 were assigned to each week in which fishery personnel had recorded the respective standard category of low, medium, or high water level during the recreational fishery. These values were averaged to provide an estimate of water level for each year. All data pertaining to the Gander River fishery, including water levels, were obtained from Moores and Tucker (1980, 1981), Moores and Ash (1984), Ash and Tucker (1984), and unpublished data provided by M. F. O'Connell and E. G. M. Ash (Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld. A1C 5X1). Least-squares regression analysis, using the best fitting (highest r value) of either arithmetic or logarithmic (base 10) functions, and analysis of variance (Dixon and Massey 1969) were employed for predictive and comparative purposes.

Results

Number, total weight, and age composition of salmon in Headwater Pond (Table 1) and Spruce Pond (Table 2) were indicative of a usual fall to spring upstream dispersion of small, young fish from the large spawning area downstream of Spruce Pond and a usual spring to fall downstream migration of smolts from the lakes. With few exceptions, numbers and total weights in both lakes increased from fall to spring and decreased from spring to fall. Ages ranged from 1 to 7 yr in both lakes, but as a result of their lesser distance from the spawning areas, fish captured in Spruce Pond had a lesser mean age than their counterparts in Headwater Pond (ANOVA, $F = 176.24$, df = 1, $p = 0.0001$). Both the number and total weight of salmon in Headwater Pond were less than those of Spruce Pond salmon in corresponding periods, and because of the twofold differences in lake size, these differences were much more apparent on an areal basis (Fig. 1). Biomass varied closely with

TABLE 1. Population size, weight, and age composition of Atlantic salmon in Headwater Pond each spring and fall, 1978–83. Shown in parentheses below the population estimate, the number of fish in each age-group, and the mean age are the 95% confidence interval, the percentage at each age, and the standard deviation, respectively.

Date of population estimate	Population estimate	Total weight (g)	Mean weight (g)	Number of fish in age-group							Mean age (yr)
				1	2	3	4	5	6	7	
May 18–30, 1979	2065 (1890–2273)	92 980	45		194 (9.4)	1352 (65.5)	459 (22.2)	58 (2.8)	2 (0.1)		3.19 (0.63)
September 12 – October 2, 1979	622 (518–779)	38 433	62		78 (12.6)	337 (54.1)	160 (25.8)	47 (7.6)			3.28 (0.78)
May 18 – June 6, 1980	1520 (1367–1713)	106 648	70	7 (0.5)	30 (2.0)	348 (22.9)	859 (56.5)	267 (17.6)	9 (0.6)		3.91 (0.74)
September 10–24, 1980	563 (436–793)	48 494	86	2 (0.4)	91 (16.2)	178 (31.6)	253 (44.9)	39 (6.8)			3.42 (0.85)
May 14–27, 1981	668 (592–766)	26 539	40		78 (11.6)	381 (57.1)	182 (27.3)	27 (4.1)			3.24 (0.71)
September 16 – October 1, 1981	382 (249–819)	19 376	51	10 (2.7)	132 (34.5)	203 (53.1)	30 (8.0)	7 (1.8)			2.72 (0.72)
May 19 – June 2, 1982	965 (845–1125)	45 718	47		115 (11.9)	265 (27.4)	430 (44.6)	125 (13.0)	26 (2.7)	4 (0.4)	3.68 (0.96)
September 15 – October 5, 1982	551 (345–1361)	29 461	54	9 (1.7)	90 (16.2)	122 (22.2)	259 (47.0)	71 (12.8)			3.53 (0.97)
May 18–27, 1983	394 (284–643)	13 682	35	10 (2.5)	158 (40.1)	191 (48.4)	30 (7.6)			5 (1.3)	2.68 (0.82)
September 14–29, 1983	521 (328–1265)	16 101	31	9 (1.7)	208 (40.0)	269 (51.7)	35 (6.7)				2.63 (0.63)

TABLE 2. Population size, weight, and age composition of Atlantic salmon in Spruce Pond each spring and fall, 1979–83. Shown in parentheses below the population estimate, the number of fish in each age-group, and the mean age are the 95% confidence interval, the percentage at each age, and the standard deviation, respectively.

Date of population estimate	Population estimate	Total weight (g)	Mean weight (g)	Number of fish in age-group							Mean age (yr)
				1	2	3	4	5	6	7	
May 18–26, 1978	2871 (2557–3273)	100 419	35	29 (1.0)	1085 (37.8)	851 (29.6)	775 (27.0)	131 (4.6)			2.96 (0.93)
September 14 – October 6, 1978	1198 (1006–1480)	44 621	37	36 (3.0)	433 (36.1)	409 (34.1)	182 (15.2)	129 (10.8)	9 (0.8)		2.97 (1.06)
May 18–25, 1979	2755 (2516–3044)	123 280	45		485 (17.6)	1344 (48.8)	761 (27.6)	151 (5.5)	7 (0.3)	7 (0.3)	3.23 (0.83)
September 12–28, 1979	1328 (1091–1695)	62 688	47	69 (5.2)	286 (21.6)	545 (41.0)	189 (14.2)	178 (13.4)	61 (4.6)		3.23 (1.21)
May 19 – June 6, 1980	1943 (1782–2135)	92 922	48	2 (0.1)	351 (18.1)	518 (26.7)	852 (43.9)	212 (10.9)	8 (0.4)		3.49 (0.93)
September 10–24, 1980	1592 (1279–2107)	79 179	50	131 (8.2)	502 (31.6)	561 (35.2)	343 (21.5)	55 (3.5)			2.81 (0.98)
May 16–27, 1981	1725 (1537–1965)	55 744	32		185 (10.8)	1028 (59.6)	419 (24.3)	93 (5.4)			3.24 (0.71)
September 16 – October 1, 1981	1949 (1626–2432)	66 473	34	171 (8.8)	702 (36.0)	982 (50.4)	91 (4.7)	3 (0.2)			2.51 (0.73)
May 18 – June 1, 1982	2112 (1955–2297)	96 220	46	12 (0.6)	268 (12.7)	463 (21.9)	868 (41.1)	326 (15.5)	175 (8.3)		3.83 (1.11)
September 15 – October 5, 1982	874 (736–1087)	32 233	37	21 (2.4)	335 (38.4)	312 (35.7)	128 (14.6)	65 (7.4)	13 (1.4)		2.91 (1.03)
May 18–26, 1983	1209 (1002–1523)	30 291	25	60 (4.9)	633 (52.4)	416 (34.4)	76 (6.3)	19 (1.6)	5 (0.4)		2.48 (0.79)
September 16–29, 1983	759 (557–1190)	24 681	33	43 (5.6)	295 (39.0)	378 (49.8)	43 (5.6)				2.56 (0.69)

density in both lakes (Fig. 1), but because of variation in age composition, the average weight of salmon varied twofold or more during the course of the study (Tables 1 and 2).

The increase in the number of salmon that occurred in both lakes each fall to spring, with the exception of Headwater Pond from 1982 to 1983, was primarily due to a net movement into the lakes of varying numbers of individuals in age-groups 1, 2, and 3 (Fig. 2 and 3). Lesser numbers of fish were calculated to have entered the lakes as members of age-groups 0, 4, 5, and 6 over the fall to spring period, but changes in the numbers of the older individuals were generally in the direction of a decrease in numbers.

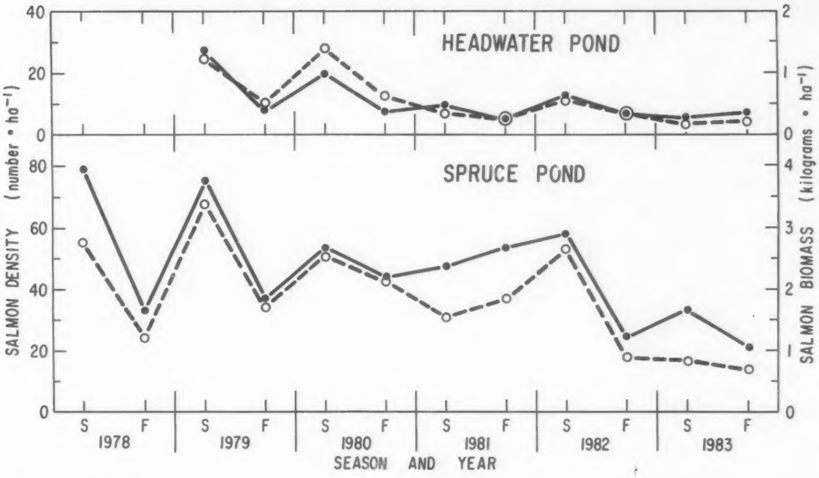

FIG. 1. Atlantic salmon density (solid points) and biomass (open points) estimates for the study lakes each spring (S) and fall (F).

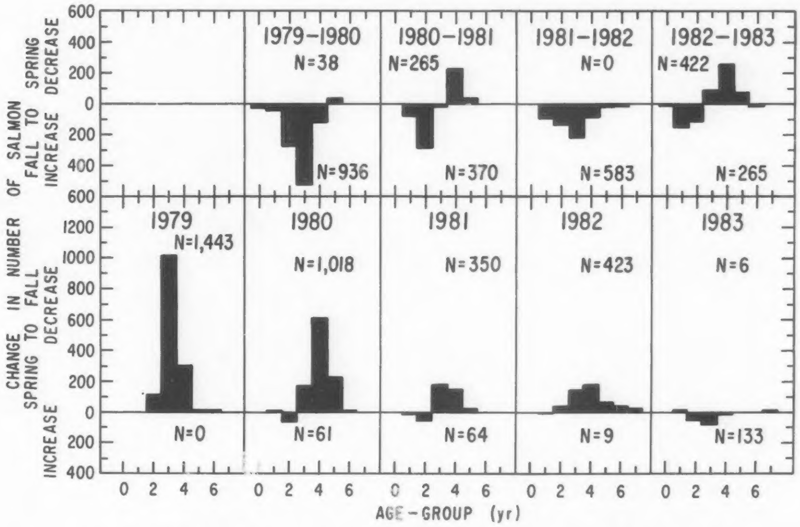

FIG. 2. Changes in the age composition of Atlantic salmon in Headwater Pond.

The decrease in the number of salmon that occurred in both lakes each spring to fall, with the exceptions of Headwater Pond in 1983 and Spruce Pond in 1981, was primarily due to a net loss from the lakes of varying numbers of individuals in age-groups 2, 3, 4, and 5 (Fig. 2 and 3). Lesser numbers of fish were calculated to have left the lakes as members of age-groups 1, 6, and 7. The number of individuals in age-group 1 typically increased over the spring to fall period.

Changes in the numbers of fin-clipped salmon in the lakes provided a further indication of the dynamic nature of fish movements. Only a small proportion of the fish marked in the spring of 1982 was subsequently recovered (Table 3). Three individuals marked in Headwater Pond were recovered in the fall in Spruce Pond. Thus, some of the calculated changes in age composition in the study lakes (Fig. 2 and 3) were due to interlake movements.

Combining the age composition data from both lakes (Fig. 4) compensated for the interlake movements and thereby revealed consistent patterns in overall fish movements into and from lake environments. The number of salmon inhabiting lake environments increased from fall to spring and decreased from spring to fall. The age composition and the dominant age-group of salmon in both lakes combined varied seasonally and annually. As in the individual lakes, the components of these changes (Fig. 5) consisted primarily of a net movement of young salmon into lake environments from fall to spring and a net loss of older fish from spring to fall. Both the number and age composition of migrating fish varied from year to year.

The magnitude of the calculated net emigration from the study lakes each spring to fall was indicative of the magnitude of the smolt run to the ocean, as shown by its relationship to the abundance of adult sea-run fish returning to the Gander River

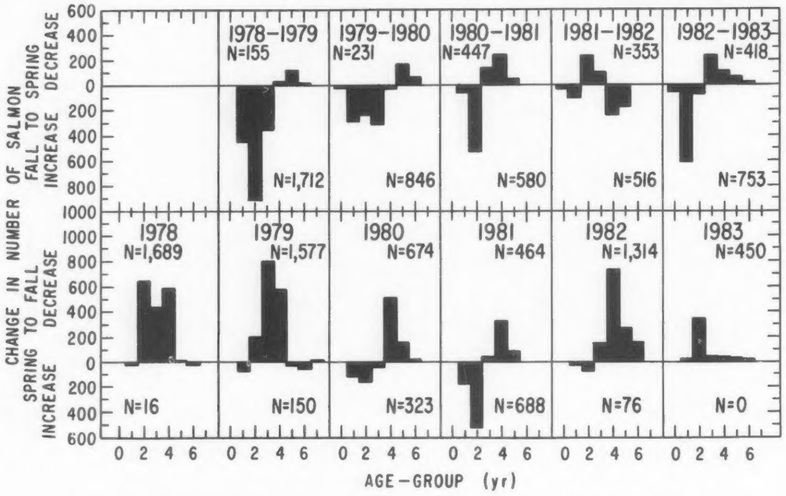

FIG. 3. Changes in the age composition of Atlantic salmon in Spruce Pond.

TABLE 3. Percentages of fin-clipped fish in the study lakes after marking in the spring of 1982. Percentages were calculated as the portion of each population clipped in the spring of 1982 and, subsequently, as the portion of clip recaptures in each catch.

	1982		1983	
	Spring	Fall	Spring	Fall
Headwater Pond	57.4	2.9[a]	0.6	0.0
Spruce Pond	65.3	0.2	0.0	0.0

[a] Does not include three fish recovered in Spruce Pond.

1 yr later (Fig. 6). Grilse abundance, as measured by angling catch per unit effort, was positively related to the number of spring to fall emigrants in the preceding year from Headwater Pond (Fig. 6A) and from Spruce Pond (Fig. 6B), although this relationship was statistically significant ($p < 0.05$) only with the data of Headwater Pond. When the data of both lakes were combined for the period 1979–83 (from Fig. 5), to compensate for interlake movements, grilse abundance in the subsequent year (Y) was positively related to the number of spring to fall emigrants (X) but, with few data points, the trend ($\log Y = 0.302 \log X - 0.594$) was not significant ($r = 0.813$, $p = 0.09$). To obtain an estimate of emigration from both lakes in 1978, thereby increasing the sample size, the number of spring to fall emigrants from both lakes (Y) was regressed on the number from Spruce Pond (X) for the period 1979–83. The resulting significant relationshp ($Y = 1.758X - 66.399$, $r = 0.899$, $p < 0.05$) was used to estimate the number of spring to fall emigrants from both lakes in 1978. With the inclusion of this estimate, grilse abundance was significantly correlated with the number of spring to fall emigrants from the study lakes as a whole (Fig. 6C).

That this relationship was indicative of a direct effect of smolt production on adult abundance was further supported by the fact that, given a similar calculated number of emigrants from the study lakes, the catch per unit effort of grilse the

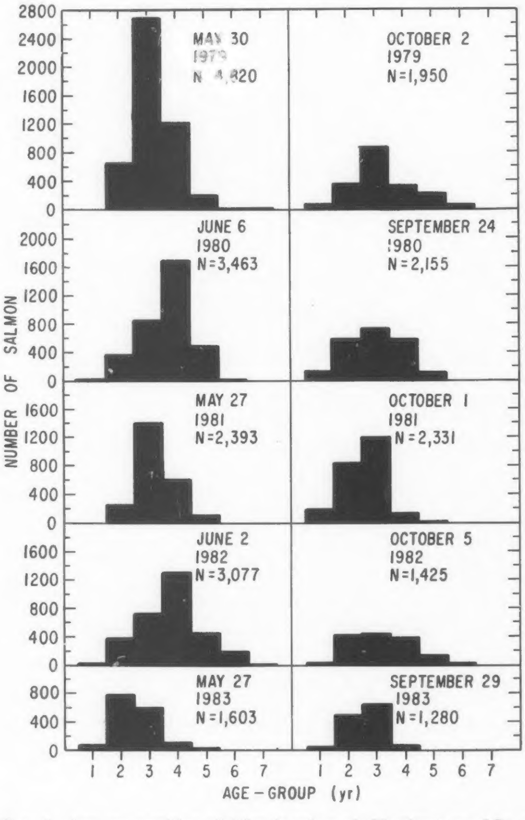

FIG. 4. Age composition of Atlantic salmon in Headwater and Spruce ponds as a whole at the end of population estimates each spring and fall, 1979–83.

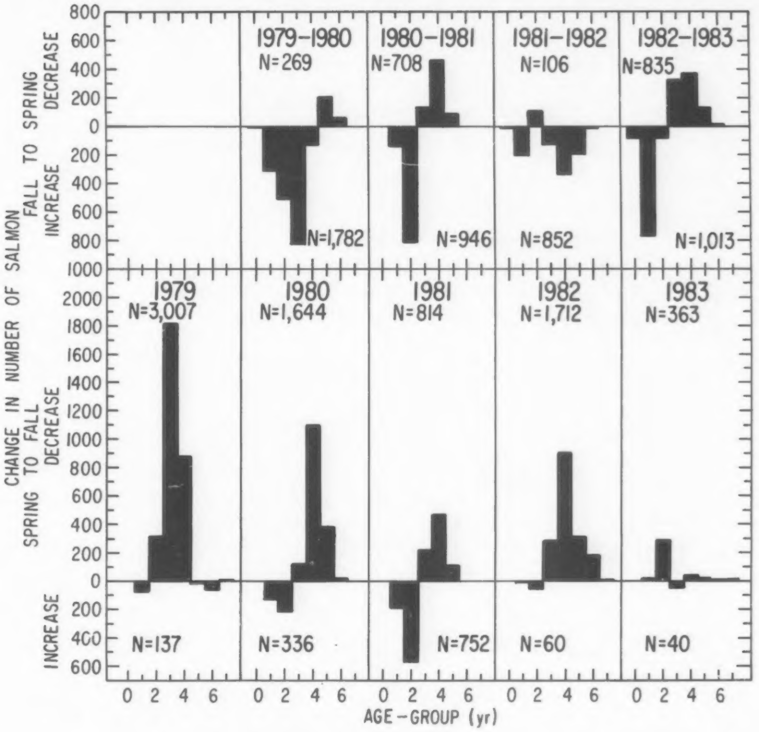

FIG. 5. Changes in the age composition of Atlantic salmon in Headwater and Spruce ponds as a whole.

following year was greater when water levels were lower, thereby compensating for some of the deviations from the regression line (Fig. 6 C). In addition, the modal ages of emigrants from the study lakes were identical to the modal river ages of grilse captured in the Gander River 1 yr later (Fig. 7).

Discussion

Population Structure

Only one previous population estimate of naturally occurring anadromous Atlantic salmon in a lake has been published. Pepper (1976) reported that the population density of parr in a lake on the Gander River system was 66 fish · ha^{-1}, corresponding to 0.57 kg · ha^{-1}, during a Schnabel estimate made over the June to September period. Pepper was unable to quantify movement to and from the lake but found, similar to the present study, that parr densities in the tributaries became dramatically reduced from May to October.

The age composition of Atlantic salmon in the study lakes is consistent with previously published work. Tributaries of the Gander River system sampled by Andrews (1965) in June, July, and August of 1951 yielded salmon predominantly of age-groups 2, 3, and 1, respectively. Few fish in age-groups 4 to 7 were captured. Pepper (1976) found age-groups 1 to 4 in his study lake on the Gander River and age-groups 0 to 4 in its tributaries. Elsewhere in eastern Canada, freshwater ages of Atlantic salmon in anadromous populations have been recorded as high as 6 yr in the Matamec River, Quebec (Gibson 1983), 7 yr in the northern part of insular Newfoundland (Chadwick et al. 1978), and 8 yr in Ungava Bay (Power 1969).

Movements to and from Lakes

The calculated changes in the age composition of salmon in the study lakes cannot be considered as precise estimates of the number of fish moving into or out of the lakes, as these estimates are subject to the uncertainty associated with mortality occurring between census periods. Mortality rates may have been variable as a result of varying amounts of stress due to high temperature (Garside 1973) or variation in growth rate and the incidence of precocious maturation (Dalley et al. 1983; Myers 1984). However, as a result of the internal consistencies of the data and the correspondence of the calculated values to external events such as the abundance and age composition of adult fish in the fishery, valuable inferences can be drawn.

The usually observed increase in the number of young fish in the study lakes over the fall to spring period (Fig. 5) represents an upstream dispersion of fish similar to that reported by Huntsman (1945), although the fish of the present study may also have travelled some distance downstream prior to their migration into the lakes. Only 10 m^2 of Atlantic salmon spawning habitat was found upstream of Spruce Pond's outlet, while, in contrast, over 1000 m^2 of spawning habitat was found within 2.2 km downstream (Ryan and Wakeham 1984). Approximately 4.9 ha of additional spawning habitat exists on the main stream within 18 km of Spruce Pond (Traverse 1972). In spite of the intensive netting of the two study lakes, only two sea-run

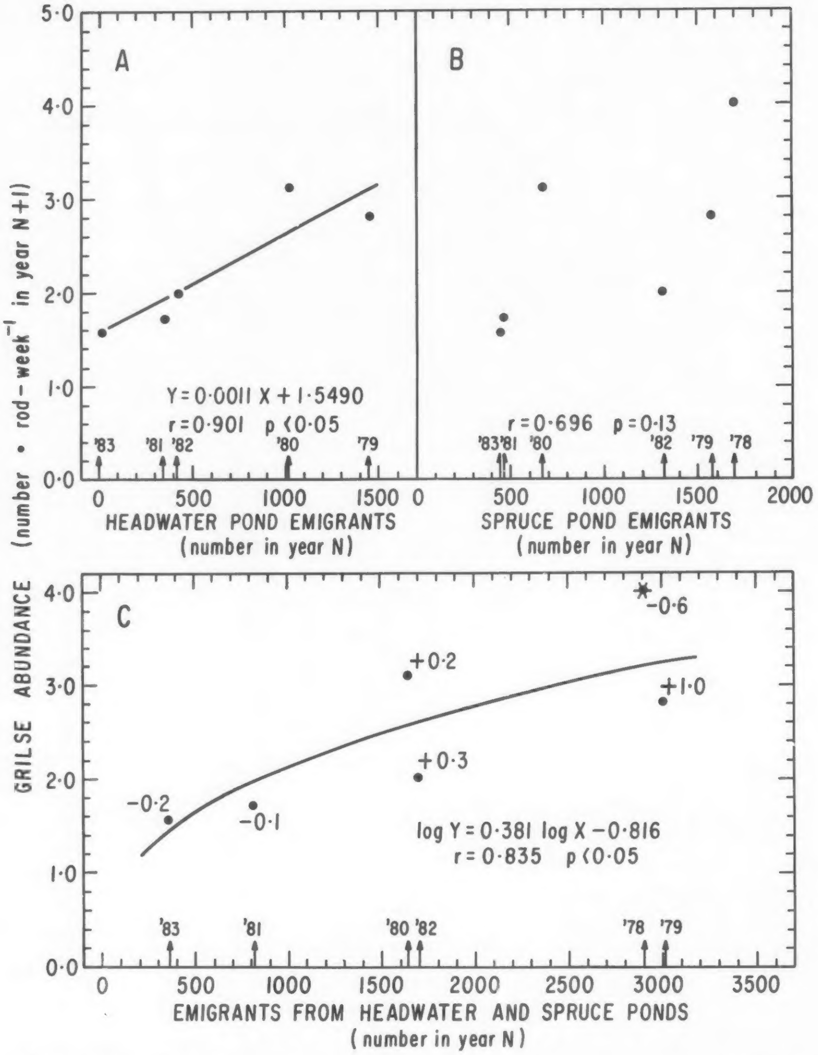

FIG. 6. Relationship of observed grilse abundance in the Gander River angling fishery to the net number of salmon migrating from (A) Headwater Pond, (B) Spruce Pond, and (C) both lakes as a whole in the spring to fall period of the preceding year. The number of emigrants in 1978 in Fig. 6C (asterisk) was calculated from the relationship of total emigrants to Spruce Pond emigrants, 1979–83. Years of emigration are indicated. Numerals beside points in Fig. 6C indicate river water levels during the grilse fishery with greater positive and negative deviations from zero representing, respectively, higher and lower water levels.

salmon were captured in Spruce Pond.

The usual decrease in the number of older fish in the lakes over the fall to spring period (Fig. 5) was likely due to mortality and the downstream dispersion of fish often observed in presmolt and nonanadromous salmonids (Ruggles 1980). Buck and Youngson (1982) have suggested that the downstream autumn migration of immature and mature Atlantic salmon parr they observed in a Scottish river may be a general phenomenon related to the movement of precocious males to the spawning grounds or environmental cues. In one tributary of the Gander River, the proportion of mature male parr has been reported as 74% (Dalley et al. 1983) to 85% (Pepper 1976). In Newfoundland, few precocious males eventually smoltify and go to sea (Chadwick 1981; Dalley et al. 1983; Myers 1984).

Relationship to Adult Returns

It is reasonable to conclude that the calculated net downstream emigration from lake environments over the spring to fall period and the age composition of its members (Fig. 5) were indicative of the relative magnitude and, to a lesser extent, the dominant age characteristics of the smolt run from the Gander River system. The positive relationship between the calculated number of emigrants from the study lakes over the spring to fall period and the abundance of one-sea-winter fish

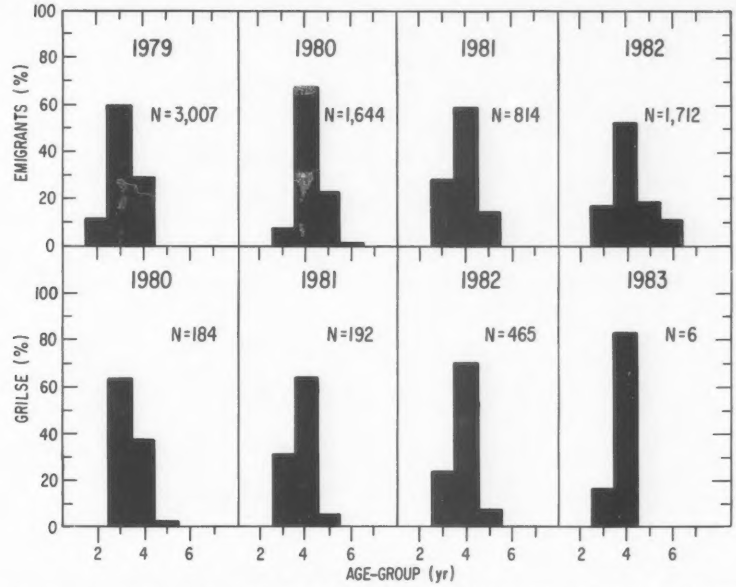

FIG. 7. Age composition of the spring to fall emigrants from Headwater and Spruce ponds (from Fig. 5) compared with the composition of river ages (freshwater life) of adults captured in the Gander River angling fishery the following year. Data for 1984 grilse are not available.

returning the following year (Fig. 6C) is characteristic of the relationship between the size of the smolt run and the number of returning grilse in Western Arm Brook, the only entire Newfoundland river system where complete counts of smolts and adults have been obtained (Chadwick et al. 1978). It has been shown that the recreational catch of grilse is positively related to their abundance (Chadwick 1982b) and the abundance of smolts the preceding year (Chadwick 1982a). Furthermore, Chadwick (1982a, 1982b) has reported that the catchability of grilse in the recreational fishery on two river systems is inversely related to summer discharge, as was indicated by the data of the present study. Similarly, the correspondence of the modal ages of the spring to fall emigrants from the study lakes from 1979 to 1982 to the modal river ages of grilse returning to the Gander River system 1 yr later is also characteristic of smolt and grilse river ages in Western Arm Brook (Chadwick et al. 1978). This pattern was also observed in Newfoundland's largest river system where only part of the stock was susceptible to sampling, but where modal smolt ages varied with changing stock densities during enhancement programs (O'Connell et al. 1983).

The lack of an exact correspondence of the age composition of the spring to fall emigrants and the river-age composition of the grilse is not atypical in comparison with other salmon rivers (Lear and Day 1977; Chadwick et al. 1978; O'Connell et al. 1983), but it is suggestive of an overestimate of the size of the smolt run from the study lakes in some years. None of the grilse captured from 1980 to 1983 had river ages of 2, 6, or 7, while some fish calculated to have left the lakes from 1979 to 1982 were members of these age-groups. Fish of these age-groups have been observed, typically in small numbers, in the smolt run in other Newfoundland rivers (Lear and Day 1977; Chadwick 1981; O'Connell et al. 1983), and there is evidence that sea survival varies inversely with smolt age (Chadwick et al. 1978). However, it is likely that part of the decrease in the number of fish in these age-groups over the spring to fall period was due to such factors as the high incidence and mortality of mature male parr in the Gander River system (Pepper 1976; Dalley et al. 1983), a downstream migration, as autumn approached, of immature and mature male parr such as described by Buck and Youngson (1982), and an upstream migration to areas between the study lakes.

It is possible that some smolts may have left the study lakes prior to the start of the spring population estimates of some years, thus resulting in an underestimate of the size of the smolt run. If this occurred, it is likely that it was, for the most part, only a minor source of error. The strong correlation between catch per unit effort and population estimate (Ryan 1984a) and the close correspondence between marking and recapture rates are indicative of, for practical purposes, closed populations during the censuses (Ricker 1975). Fish in the lakes during the censuses were not observed to have attained the silvering and loss of parr marks characteristic of migrating smolts in the nearby Exploits River. In the Exploits River, peak smolt movement generally occurs in early to late June (O'Connell et al. 1983). However, the modal age of 2 in the spring to fall decrease from the study lakes in 1983 is suggestive of an underestimate of the smolt run in that year, since grilse having two river years were not captured from 1980 to 1983. Fish of the 1983 smolt run may have prematurely left or have been prevented from entering the study area due to unusual environmental conditions prior to the spring census of 1983. In January of that year, an exceptionally high rainfall occurred. Over 23 cm of rain fell during 48 h on the south coast of Newfoundland (Anonymous 1983) and resultant floods washed out road culverts downstream of the study area. Accordingly, the calculated spring to fall emigration from the study area should be considered as indicative of the relative magnitude of the smolt run rather than a precise measure of its absolute size.

That the number of spring to fall emigrants from the study area is a significant predictor of the subsequent abundance of adults returning to the Gander River system as a whole suggests that the factors determining smolt production vary in a similar manner throughout different sections of the Gander River system. The catchment basin of the study area, 20.1 km^2 (Ryan and Wakeham 1984), is only 0.3% of the catchment basin of the Gander River in its entirety (Traverse 1972). In addition, the Atlantic salmon spawning habitat in the outlet from Spruce Pond within 18 km of the study area is only about 2.5% of the total spawning habitat of the Gander River system (Traverse 1972). These results are consistent with Chadwick's (1982c) evidence that the freshwater survival of salmon is similar on very different watersheds.

Lake Production

It is not possible to obtain a precise estimate of salmon production in lake environments from data of the present study due to the long time between censuses and the previous stream habitation of the fish censused in lake environments. Similar constraints applied to Chadwick and Green's (1985) estimate of lacustrine salmon production in Western Arm Brook, Newfoundland, which was based on the difference between total river system production and stream production. These authors stressed that their estimate of $0.07\ g\cdot m^{-2}\cdot yr^{-1}$ was very preliminary and probably an overestimate as a result of an underestimate of production in stream habitats. In the present study, the calculated number of spring to fall emigrants from the two lakes as a whole from 1979 to 1983 averaged 1508 fish to 13.4 $fish\cdot ha^{-1}$. Based on the mean weight of all salmon censused in both lakes each spring from 1979 to 1983, this corresponds to an average annual spring emigration of $0.06\ g\cdot m^2$ lake habitat^{-1}. Since a large part of the growth of these fish must have occurred in stream environments, it appears that lacustrine Atlantic salmon production in Western Arm Brook tends to be greater than in Headwater and Spruce ponds. Lakes of Western Arm Brook are shallower and less dilute (Chadwick and Green 1985) than Headwater and Spruce ponds and thus potentially more productive (Ryder 1982).

Research Implications

It is probable that the spring and fall censusing of a larger area and a variety of habitats greater than considered in the present study would result in a stronger correspondence between the spring to fall emigration of young salmon from freshwaters and the resultant abundance of adults. For example, grilse abundance in the Gander River was not significantly related to the number of spring to fall emigrants from both of the study lakes on an individual basis, and the age composition of emigrants from both lakes as a whole resembled the composition of grilse river ages more than did the age composition of emigrants from the individual lakes. The consideration of both lakes as a whole compensated somewhat for movement between the two lakes and resulted in a more appropriate correspondence of lake emigrant characteristics to the characteristics of grilse returning the following year.

The representative sampling of all habitat types for juvenile Atlantic salmon as an aid in the prediction of smolt production has been suggested by Marshall (1983). It is apparent that representative habitat types for juvenile Atlantic salmon include standing waters, at least in Newfoundland. Results of the present study suggest that the techniques described herein can be used in the standing waters of other river systems to assist in the monitoring of smolt production and in the prediction of the subsequent abundance of adults.

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Effects of Temperature and Food Quality on Growth and Development of a Mayfly, *Leptophlebia intermedia*

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Sweeney, B. W., R. L. Vannote, and P. J. Dodds. 1986. Effects of temperature and food quality on growth and development of a mayfly, *Leptophlebia intermedia*. Can. J. Fish. Aquat. Sci. 43: 12–18.

Larval development, adult size, and fecundity of *Leptophlebia intermedia* were assessed in response to rearing on five diets (hickory, white ash, red oak, chestnut oak, and American beech leaves) at each of three temperature regimes (ambient White Clay Creek temperatures (WCC) and 3 and 6°C above WCC). Developmental time was shortened about 40–50 d by elevating creek temperatures 6°C, but varied only about 20–30 d over the range of diets for any given temperature. Adult size was influenced more by diet than temperature. Adult female weights differed among diets by about 1.5 mg for any given temperature regime. In contrast, female weights varied by only about 0.6 mg among temperatures for any given diet. The proportion of total female weight allocated to eggs increased with adult size and ranged from 0.12 to 0.45 depending on diet and temperature. In general, hickory and white ash diets consistently yielded the highest survival and largest adults, while the highest mortality and poorest growth occurred on the red oak and American beech diets.

On a évalué la réaction de *Leptophlebia intermedia* du point de vue du développement des larves, de la taille des adultes et de la fécondité en soumettant cette espèce à cinq régimes alimentaires différents (feuilles de caryer, de frêne d'Amérique, de chêne rouge, de chêne châtaignier et de hêtre à grandes feuilles) à chacun des trois régimes de température (températures ambiantes du ruisseau White Clay (RWC) et températures de 3 et 6°C supérieurs à celles du RWC). Le temps de croissance a été réduit de 40 à 50 jours en élevant la température du ruisseau de 6°C mais n'a varié que de 20 à 30 jours environ pour toute la gamme de régimes alimentaires à n'importe quelle température. Le régime alimentaire a influé davantage sur la taille des adultes que la température. Le poids des femelles adultes différait selon le régime alimentaire de 1,5 mg environ pour tout régime de température donné. Par contre, le poids des femelles n'a varié que de 0,6 mg environ en fonction de la température pour tout régime alimentaire donné. La partie du poids total des femelles consacrée à la formation des oeufs a augmenté proportionnellement à la taille des adultes et a varié de 0,12 à 0,45 selon le régime alimentaire et la température. De façon générale, le taux de survie a été plus élevé et les adultes étaient plus gros lorsque le régime alimentaire était constitué de feuilles de caryer ou de frêne d'Amérique, tandis que le taux de mortalité était plus élevé et la croissance plus faible avec les feuilles de chêne rouge ou de hêtre à grandes feuilles.

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The seasonal pattern of temperature and nutritive value of food significantly affects the life history characteristics of a variety of aquatic insect species (see Sweeney 1984 for review). It is difficult, however, to design experiments to adequately test the relative importance of these two factors because temperature can affect the growth and development of insect larvae both directly, through metabolic processes, and indirectly, by affecting the quantity or quality of food. Thus, most studies have focused on either temperature or food as an experimental variable, and the interaction of these two factors has only been tested to a limited extent on a few shredder and collector species (e.g. Anderson and Cummins 1979; Ward and Cummins 1979).

For aquatic detritivores, studies of food quality have largely involved rearing larvae for various lengths of time on different species of deciduous leaves (Wallace et al. 1970; Iversen 1974; Otto 1974; Grafius and Anderson 1979; Anderson and Sedell 1979). Leaf species often differ from one another in terms of biochemical composition (i.e. proportions by weight of lipids, fats, and carbohydrates) and associated microflora (i.e. quantity and quality of colonizing bacteria and fungi), both of which affect the nutritive quality of the leaves. Larval feeding and growth rates often vary significantly with the species of leaf provided as food (Cummins et al. 1973; Iversen 1974; Otto 1974; Anderson and Cummins 1979).

This paper focuses on the relative importance of temperature and nutrition to certain life history characteristics of *Leptophlebia intermedia* (Traver), a leaf-shredding mayfly. We assessed development, size, and fecundity of larvae reared on five diets (i.e. hickory, white ash, red oak, chestnut oak, and American beech leaves) at each of three temperature regimes: ambient White Clay Creek temperature (WCC) and when WCC was increased constantly by 3 and 6°C.

Materials and Methods

Test Species

Leptophlebia intermedia occurs in slow flow areas of small to intermediate streams in the eastern and southeastern region of the United States (Berner 1950, 1975). The species seems to

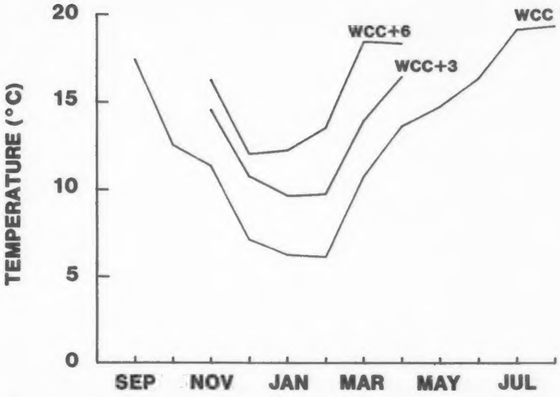

FIG. 1. Mean monthly temperatures for each of the three experimental regimes used for rearing experiments on *Leptophlebia intermedia*.

be univoltine throughout its range, with adult emergence occurring from early February in the south to late March in the north. In White Clay Creek, larvae are often found in accumulations of deciduous leaves. Although we have no direct evidence that *L. intermedia* larvae actually shred leaves in the field, we have observed it directly (visual) and indirectly (large quantities of fecal pellets in trays containing only larvae and leaves) in the laboratory. We have not attempted to determine whether *L. intermedia* prefers certain particle sizes of leaves. Larvae probably also ingest algae (diatoms) and fungi associated with the leaves in the field. The overall ecology and life history appears similar to congeneric species occurring in North America (*L. cupida* (Say): Clifford 1969, 1970a, 1970b; Clifford et al. 1978) and Europe (*L. vespertina* (L.) and *L. marginata* (L.): Brittain 1972, 1976). In White Clay Creek, larvae apparently hatch from eggs in late August and emerge as adults in late March.

Larval Growth and Adult Emergence

Larvae were collected on December 31 from first- and second-order tributaries of White Clay Creek in Londonderry township, Chester County, Pennsylvania (39°51′47″N; 75°47′07″W). They were divided into groups of 150 individuals, and each group was placed into a separate flow-through tray (23 × 45 × 22 cm deep) for rearing. One group of larvae was reared on each of the following diets at each temperature regime: American beech (*Fragus grandifolia*), chestnut oak (*Quercus prinus*), red oak (*Quercus rubra*), hickory (*Carya ovata* and *C. ovalis*), and white ash (*Fraxinus americana*). These species were carefully chosen to represent a nutritional gradient ranging from poor to good in White Clay Creek (Sweeney and Vannote 1985; Vannote and Sweeney 1985). There were three temperature regimes (Fig. 1): (i) ambient White Clay Creek temperatures (WCC); (ii) White Clay Creek warmed about 3°C (WCC + 3°C); and (iii) White Clay Creek warmed about 6°C (WCC + 6°C).

The average size of larvae at the start of the experiment was estimated by killing and dry weighing (60°C, 48 h) 100 larvae that were collected at the same time and location as the experimental larvae. Larvae were slightly less than half grown when collected on December 31 and none showed any signs of maturity (e.g. well-developed wing pads). Larvae were reared in the trays until metamorphosis. During the emergence period, subimagoes were collected daily beneath netting that was fastened tightly over each tray. Male subimagoes were killed and dry weighed. Female subimagoes (hereafter called adults) were frozen immediately and subsequently dissected to determine fecundity (see Materials and Methods).

For each temperature regime, water was pumped to the rearing trays from a separate 800-L reservoir. The diel and seasonal cycle of temperature in the creek was reproduced in the laboratory by constantly pumping creek water through Pyrex® heat exchange coils submerged in each reservoir. Aquarium heaters were used to add the 3 and 6°C of heat needed to produce the WCC + 3°C and WCC + 6°C thermal regimes. The water in each reservoir was replaced weekly with fresh stream water.

At the start of the experiment, leaves were soaked in stream water for 1 wk at 20°C and then in the rearing trays for 1 wk before adding the larvae. During the study, leaves were kept in aerated 120-L reservoirs with stream water (changed twice a week) and periodically added to trays to keep food levels nonlimiting.

Protein levels associated with each leaf diet were measured in the three thermal regimes. Each leaf type was placed into a separate mesh bag and submerged for 6 wk in each reservoir. Leaves were then removed, dried, and ground in a Wiley mill. The amount of protein was determined using the method of Lowry et al. (1951). We emphasized protein levels among diets because protein is the principal component of aquatic insect eggs which contribute greatly to the weight of mature females (Harvey et al. 1979; unpubl. data).

Fecundity

The eggs were removed, placed on a preweighed glass coverslip, dried for 48 h at 60°C, and the mass (milligrams) determined by reweighing the coverslip with attached eggs. A dry mass was also obtained on each female body after removing the eggs. The total mass of each female was estimated by summing the egg and body masses.

The number of eggs per female was estimated from egg mass with the following equation: $Y = 7.934 + 1192.2\ (X)$, where Y = number of eggs and X = mass of eggs (milligrams) ($r^2 = 0.98$). This relationship was derived by removing eggs from 10 females (two chosen at random from each of the five diets), counting out various quantities of eggs for each female (i.e. 25−1200 in increments of about 50), and obtaining the dry mass of each quantity.

Mean reproductive effort of females was estimated as described by Tinkle and Hadley (1975). Reproductive effort in this context refers to the ratio of egg biomass to total female biomass (including eggs).

Results and Discussion

Larval Mortality

Mortality during the experiment tended to be higher on leaf species that produced small adults (chestnut oak, red oak, and American beech) and lower on diets yielding large adults (hickory and white ash) for all temperature regimes (Table 1). Mortality also seemed to decrease with increased temperature on diets producing large adults (hickory and white ash) and

TABLE 1. Adult size, reproductive potential, and emergence of *Leptophlebia intermeida* reared on five leaf diets at three experimental HI = hickory, WA = white ash, RO = red oak, CO = chestnut oak, AB = American beech.

		Adult dry weight (mg)											
		Male				Female				No. of eggs per female			
Temperature regime	Leaf diet	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range
WCC	HI	14	1.90	0.47	1.29–2.65	16	3.70	1.14	1.34–5.22	12	1064	471	28–1507
	WA	17	2.51	0.42	1.52–3.07	11	3.27	0.90	2.10–4.89	6	831	480	469–1388
	RO	11	1.37	0.17	1.09–1.68	6	1.69	0.51	1.22–2.66	3	272	470	0–815
	CO	18	1.48	0.34	0.79–2.13	17	1.82	0.50	1.22–2.14	9	223	188	0–553
	AB	12	1.36	0.14	1.18–1.65	8	1.63	0.41	1.07–2.18	6	212	156	0–410
WCC + 3°C	HI	40	2.01	0.34	1.37–2.92	34	3.23	0.90	1.93–5.29	26	939	474	159–1996
	WA	27	2.30	0.63	1.13–3.42	27	3.91	1.09	2.22–6.04	22	1079	588	183–2265
	RO	11	1.55	0.37	1.12–2.38	6	1.92	0.96	1.14–3.46	3	732	312	446–1066
	CO	11	1.73	0.36	1.03–2.34	12	3.11	1.14	1.77–5.77	11	787	613	0–2163
	AB	6	1.66	0.35	1.32–2.06	6	2.67	1.31	1.38–5.00	6	641	733	0–1996
WCC + 6°C	HI	24	2.06	0.40	1.55–2.88	34	2.61	0.52	1.60–3.80	28	479	349	3–1412
	WA	12	2.31	0.45	1.35–2.78	25	3.80	1.16	1.92–6.55	21	1329	643	116–2748
	RO	5	1.47	0.13	1.27–1.58	5	2.84	1.18	1.39–4.16	4	865	742	1–1531
	CO	4	1.66	0.39	1.43–2.23	6	2.65	1.28	1.59–4.84	5	774	775	0–1948
	AB	2	1.17	0.23	0.99–1.34	2	2.04	0.57	1.64–2.44	1	307	—	307

increase with temperature on diets producing small adults (red oak, chestnut oak, and American beech). There was, however, no statistical correlation between daily mortality rate and either larval growth rate, adult size, or developmental time.

Larval Development

The amount of time needed to complete larval growth (i.e. developmental time) was affected significantly by both temperature and diet. Larvae of both sexes completed development and emerged as adults earlier from the WCC + 3°C and WCC + 6°C regimes relative to WCC (Table 1). For example, females completed development 38–54 d earlier (depending on diet) at WCC + 6°C than at ambient WCC. Mean developmental time of both sexes significantly decreased with increased temperature for the hickory, white ash, chestnut oak, and American beech diets (ANOVA, Scheffe test, $p < 0.05$; see Table 2). Mean developmental time for larvae on the red oak diet was statistically the same for the ambient WCC and WCC + 3°C regimes but significantly shorter for WCC + 6°C (ANOVA, Scheffe test, $p < 0.05$). Results from a two-way ANOVA comparing all diets and temperatures revealed no significant interaction of temperature and diet on mean developmental time.

A significant diet effect was observed for mean developmental time at each of the three temperature regimes (ANOVA, $p < 0.05$). The only consistent pattern, however, was the significantly shorter mean development time for hickory and/or white ash relative to the other diets (Scheffe test; Table 3). In general, the response of developmental time to diet was substantially less than the response to temperature, even though temperature regimes differed by 6°C or less and the range of diets was deliberately chosen to include a gradient from good to poor in terms of overall nutrition or growth response. For example, the fastest and slowest median developmental time differed on the average by about 37% among diets for a given temperature regime. In comparison, the fastest and slowest median developmental time differed on the average by about

TABLE 2. Results of Scheffe multiple range tests used to compare the relative effects of temperature within a given diet on developmental time, adult biomass, and fecundity for *Leptophlebia intermedia*. Although each leaf diet was tested separately, diets are presented together when the results were identical. Temperature regimes connected by solid lines did not differ significantly for the parameter being tested. The broken line connects two temperatures that did not differ significantly but could not be presented in adjacent columns. a = insufficient data for statistical comparison.

<table>
<tr><th></th><th colspan="3">Temperature regime</th></tr>
<tr><th>Leaf diets</th><th>WCC</th><th>WCC + 3°C</th><th>WCC + 6°C</th></tr>
<tr><td></td><td colspan="3"><i>Developmental time (females)</i></td></tr>
<tr><td>HI, WA, CO</td><td>————</td><td>————</td><td>————</td></tr>
<tr><td>RO</td><td colspan="2">————————</td><td>————</td></tr>
<tr><td>AB</td><td>————</td><td>————</td><td>a</td></tr>
<tr><td></td><td colspan="3"><i>Developmental time (males)</i></td></tr>
<tr><td>HI, WA, RO, CO</td><td>————</td><td>————</td><td>————</td></tr>
<tr><td>AB</td><td>————</td><td>————</td><td>a</td></tr>
<tr><td></td><td colspan="3"><i>Adult female biomass (mg)</i></td></tr>
<tr><td>HI</td><td colspan="2">————————</td><td>————</td></tr>
<tr><td>WA, RO</td><td colspan="3">————————————</td></tr>
<tr><td>CO</td><td>————</td><td>- - - - - -</td><td>————</td></tr>
<tr><td></td><td></td><td colspan="2">————————</td></tr>
<tr><td>AB</td><td colspan="2">————————</td><td>a</td></tr>
<tr><td></td><td colspan="3"><i>Adult male biomass (mg)</i></td></tr>
<tr><td>HI, WA, RO, CO</td><td colspan="3">————————————</td></tr>
<tr><td>AB</td><td>————</td><td>————</td><td>a</td></tr>
<tr><td></td><td colspan="3"><i>Fecundity</i></td></tr>
<tr><td>HI</td><td colspan="2">————————</td><td></td></tr>
<tr><td>WA, RO, CO</td><td colspan="3">————————————</td></tr>
<tr><td>AB</td><td colspan="2">————————</td><td>a</td></tr>
</table>

temperatures, beginning January 2 (initial larval size: $\bar{x} = 2.61$, SD = 1.03, range = 0.50–5.95).

Mean reproductive effort				Larval mortality (%)	Developmental time					
					Days to first adult		Days to median adult		Mean	
n	$\bar{x}$	SD	Range		Male	Female	Male	Female	Male	Female
12	0.21	0.07	0.02–0.27	80	77	83	92	97	94	96
6	0.17	0.08	0.08–0.25	81	58	92	92	97	88	102
1	0.26	—	0.26	88	83	97	118	118	118	119
7	0.11	0.05	0.05–0.18	77	97	92	112	115	113	114
5	0.12	0.05	0.06–0.18	85	92	97	118	115	114	114
23	0.21	0.07	0.07–0.32	50	54	55	77	71	74	74
20	0.21	0.06	0.07–0.30	64	54	50	70	73	73	77
3	0.22	0.04	0.18–0.26	88	90	81	103	102	103	101
10	0.21	0.07	0.12–0.32	84	77	85	90	97	95	96
4	0.22	0.10	0.10–0.34	92	85	55	90	92	93	90
4	0.22	0.03	0.20–0.27	61	43	45	55	55	54	57
7	0.31	0.03	0.26–0.35	75	43	43	50	50	53	51
2	0.31	0.03	0.29–0.33	93	59	44	69	59	70	68
3	0.26	0.09	0.16–0.34	93	56	43	69	63	70	66
—	—	—	—	97	69	43	69	43	81	44

71% among temperature regimes for a given diet. This suggests that the rate of larval development was determined largely by the seasonal pattern and magnitude of temperatures, with diet playing a modifying role.

Adult Size

The white ash and hickory diets generally produced larger male and female adults than other diets within each thermal regime (Table 1). At WCC, female adults from the white ash and hickory diets were about the same size and significantly larger than adults reared on the other diets (Table 3). The only significant differences for adult weights among diets at higher temperatures was between white ash and red oak at WCC + 3°C and white ash and hickory at WCC + 6°C. Adult males reared on white ash leaves were significantly larger than males reared on chestnut oak or red oak leaves at all temperatures, and also larger than males reared on hickory and American beech leaves at WCC. No significant differences were observed for the size of males reared on the American beech, chestnut oak, and red oak diets at any temperature. Thus, male and female adults reared on chestnut oak, red oak, and American beech leaves were about the same size at all temperatures and were generally the smallest adults produced during the experiment.

Male and female weights were significantly larger at WCC relative to WCC + 3°C when the data were combined for all diets (ANOVA, $p < 0.05$). The effects of temperature, however, varied greatly among males and females and from diet to diet. For example, female weights significantly decreased with increased temperatures for hickory leaves but significantly increased with temperatures for all other diets (Table 2). Although males reared on hickory, white ash, red oak, and chestnut oak seemed to increase in weight from ambient WCC to WCC + 3°C and then decrease at WCC + 6°C, the differences were not significant. Adult males reared on American beech were significantly larger at WCC + 3°C relative to WCC.

The data suggest that both temperature and diet can significantly affect adult size of *L. intermedia*. For females, a two-way ANOVA revealed that temperature and diet interact significantly in producing the observed changes in adult size. However, no significant interaction was observed for the males.

Fecundity

We expected a priori that fecundity would exhibit the same response pattern to temperature and diet as adult weight because of the obvious correlation between the two parameters. Although both fecundity and female size generally decreased with increased tempeature for all diets except hickory, the levels of significance of these patterns often differed for the two parameters. For example, adult females from the white ash diet were significantly heavier than females from most of the other diets at all temperatures. Fecundity levels for females reared on white ash, however, were not significantly different from any other diet at WCC + 3°C as well as most other diets at WCC (except chestnut oak and American beech) and WCC + 6°C (except hickory). Similarly, fecundity levels for the chestnut oak diet did not vary significantly among any of the temperature regimes, even though significant differences were observed for female size (Table 2).

The observed differences in the response of adult size and fecundity to temperature and/or diet are undoubtedly related to changes in the relationship between fecundity and size for each experimental population (Table 1; Table 4 contains the specific equations). A comparison of the slopes for regressions relating egg number and adult female biomass indicated significant differences among diets only for the WCC regime (ANCOVA, $p < 0.05$). A similar analysis revealed significant temperature effects on regression slopes only for the chestnut oak diet (ANCOVA, $p < 0.05$). The underlying factors causing the changes in the slopes of these regressions are unknown. We did not attempt to measure differences in mean egg size or egg mass for females from the different treatments.

TABLE 3. Results of Scheffe multiple range tests used to compare the relative effects of diet within a given temperature regime on developmental time, adult biomass, and fecundity for *Leptophlebia intermedia*. Diets connected by a solid line did not differ significantly for the parameter being tested. The broken line connects two diets that did not differ significantly but could not be presented in adjacent columns. a = insufficient data for statistical comparison.

Temperature regime	Leaf diets				
	HI	WA	AB	RO	CO
			Developmental time (females)		
WCC	———	———			
		———	———	———	———
WCC + 3°C	———	———	———		
			———	———	———
WCC + 6°C	———	———			
	———	- - -	a	———	———
			Developmental time (males)		
	HI	WA	CO	RO	AB
WCC	———	———	———	———	———
WCC + 3°C	———	———	———	———	———
WCC + 6°C	———	———	———	———	a
			Adult female biomass (mg)		
	WA	HI	AB	CO	RO
WCC	———	———	———	———	———
WCC + 3°C	———	———	———	———	
		———	———	———	———
WCC + 6°C	———	- - -	a	———	———
		———	a	———	———
			Adult male biomass (mg)		
	WA	HI	AB	CO	RO
WCC	———	———	———	———	———
WCC + 3°C	———	———	———		
		———	———	———	———
WCC + 6°C	———	———	a	———	
				———	———
			Fecundity		
	HI	WA	RO	CO	AB
WCC	———	———	———		
		———	———	———	———
WCC + 3°C	———	———	———	———	———
WCC + 6°C	———	- - - ———	———	———	
		———	———	———	a

The proportion of total female weight allocated to eggs (i.e. reproductive effort) ranged from 0.12 to 0.45 depending on diet and temperature (Table 1). Reproductive effort (RE) generally increased with temperature (e.g. overall average RE for WCC, WCC + 3°C, and WCC + 6°C was 0.21, 0.28, and 0.39, respectively) and adult size (correlation coefficient = 0.78, $p < 0.001$; Fig. 2). It appears that in nonoptimal conditions, a premium is placed on attaining a certain physical adult size, even if only a small amount of energy can be allocated to reproduction. In optimal conditions for growth, larvae attain a certain size and then allocate disproportionately large amounts of energy to eggs rather than further increasing in size.

Conclusions

A few general conclusions can be made concerning the nutritive quality of the five diets that were tested. Hickory and white ash, which consistently resulted in the highest survival and best overall larval growth regardless of temperature, seemed to provide superior nutrition to larvae relative to the other leaf diets. In contrast, the consistently high mortality and poor larval growth associated with red oak and American beech diets suggest a low nutritive quality. Protein levels were substantially higher for hickory and white ash relative to other diets but protein levels were not checked throughout the experiment and we do not know what proportion of the protein was associated with live (microbes) versus dead (leaf) biomass.

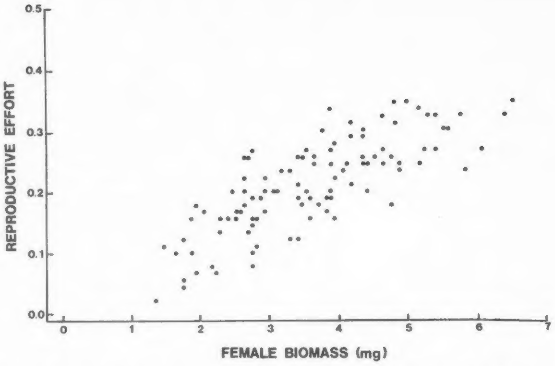

FIG. 2. Reproductive effort of *Leptophlebia intermedia* (total egg biomass/total adult female biomass including eggs) versus adult female biomass.

It is unclear whether diet is generally more important than temperature with respect to larval growth and adult size of *L. intermedia*. In these experiments, five diets were deliberately chosen to represent a nutritional range from poor to good (based on laboratory results on other aquatic species). Our design, however, did not include a range of temperature regimes from lower lethal to upper lethal for comparison. Our experimental temperature regimes differed at most by only 6°C (e.g. WCC vs. WCC + 6°C) but the actual temperatures when larvae did most of their growth probably differed by less than 6°C. For example, adding 6°C in midwinter to natural stream temperatures caused larvae to resume growth and emerge about 7 wk earlier than normal. At natural winter temperatures, larvae are in a facultative diapause and do not grow; growth resumes only after temperatures rise to about 10°C. In the WCC regime, larvae did most of their growth several weeks later than larvae in the WCC + 6°C regime but probably at comparable temperatures. Thus, the experimental design was biased towards evaluating the absolute effect of diet (not temperature) on larval growth and adult size and fecundity of *L. intermedia*.

The results of this experiment strongly suggest that (i) temperature is the principal factor determining the overall length of the larval growth period and (ii) the ultimate size that a given larva attains (i.e. adult size) depends on how fast and efficiently it can grow in the available time period. Our experiment confirms that diet can strongly influence the magnitude of growth (see Anderson and Cummins 1979). However, the full effects of temperature on the growth of this species still need to be properly tested.

The data base on *L. intermedia*, and for aquatic insects in general, needs to be expanded considerably before speculating on the relative importance of temperature and nutrition to the life history characteristics and geographic dispersal of aquatic

TABLE 4. Parameters of regression equations ($Y = a + bX$) relating egg number (Y) to female biomass (X) in milligrams for *Leptophlebia intermedia*. Parameters are given separately for each combination of diet and temperature as well as for data combined for all diets at each temperature. Not enough data were available to perform regressions for the red oak diet at all temperatures and the American beech diet at WCC + 6°C.

Temperature regime	Diet	b	s_b	a	s_a	r^2	df	F-ratio	p
WCC	HI	394.8	43.9	−517.6	182.0	0.89	1,10	80.9	0.0001
	WA	604.9	66.0	−1463.6	254.5	0.95	1,4	84.1	0.0008
	CO	280.2	63.1	−343.1	132.1	0.73	1,7	19.7	0.0030
	AB	308.7	169.4	−340.3	307.7	0.45	1,4	3.3	0.1424
	Pooled	393.5	21.27	−552.2	69.8	0.91	1,31	342.2	0.0001
WCC + 3°C	HI	535.0	42.5	−939.3	153.1	0.86	1,24	158.5	0.0001
	WA	481.1	45.2	−886.0	191.1	0.85	1,20	113.4	0.0001
	CO	501.4	39.5	−776.3	130.5	0.94	1,9	160.8	0.0001
	AB	552.6	46.6	−833.8	136.2	0.97	1,4	140.7	0.0003
	Pooled	474.0	23.0	−753.2	85.5	0.87	1,63	426.3	0.0001
WCC + 6°C	HI	482.8	108.9	−781.2	288.6	0.43	1,26	19.7	0.0001
	WA	506.6	25.6	−642.7	104.4	0.95	1,19	391.1	0.0001
	CO	586.9	20.9	−902.4	64.6	0.99	1,3	789.1	0.0001
	Pooled	559.5	28.3	−915.2	93.4	0.88	1,52	391.9	0.0001

insects. It appears, however, that even when food quantity is nonlimiting, changes in food quality can cause significant changes in larval growth and survival. Our understanding of these processes will have direct bearing on existing models concerning environmental variation and its effect on aquatic insect populations. For example, to what degree should the thermal equilibrium hypothesis (Sweeney and Vannote 1978; Vannote and Sweeney 1980) be modified to take into account food quality along natural thermal gradients? It is certainly known that plant communities change along temperature gradients associated with latitude and/or altitude. It is unknown, however, to what degree parallel gradients of water temperature and tree species along stream corridors interact to cause observed changes in life history characteristics of resident populations.

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Influence of Dietary Protein and Lipid on Apparent Heat Increment of Rainbow Trout, *Salmo gairdneri*

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Oxygen uptake attributable to apparent heat increment (AHI) in rainbow trout, *Salmo gairdneri* (10–15 g), induced to swim at $\cong 2\ \mathrm{BL \cdot s^{-1}}$ was influenced by dietary energy intake and diet composition. Twelve balanced diets were tested, with protein levels of ≅34, 40, 48, and 60% and lipid levels of ≅7, 15, and 23% factorally combined. Diets supplying 34% protein and 23% lipid (protein to energy ratio of $94.3\ \mathrm{mg \cdot kcal^{-1}}$) resulted in the lowest AHI of all diets tested, indicating most efficient utilization of dietary protein. At a dietary lipid level of 23%, dietary protein levels lower than 34% may result in a further reduction in AHI. Duration of elevated metabolism following feeding was independent of dietary protein and lipid level, as well as dietary energy intake. AHI of rainbow trout represented the equivalent of 15–24% of the digestible energy intake, depending on diet composition. A reduction in dietary protein with a concomitant increase in dietary lipid in the formulation of feeds for aquaculture purposes could enhance growth efficiency by reducing the energy expenditure for AHI.

L'absorption d'oxygène attribuable à l'augmentation apparente de chaleur (AAC) chez la truite arc-en-ciel, *Salmo gairdneri*, (pesant entre 10 et 15 g) amenée à nager à une vitesse d'environ $2\ \mathrm{LC \cdot s^{-1}}$ a été influencée par l'apport énergétique et la composition du régime alimentaire. On a essayé 12 régimes alimentaires équilibrés, dont la teneur en protéines était d'environ 34, 40, 48 et 60 % et la teneur en lipides de 7, 15 et 23 %, éléments qui ont été combinés en usine. Les régimes alimentaires fournissant 34 % de protéines et 23 % de lipides (rapport entre les protéines et le contenu énergétique de $94{,}3\ \mathrm{mg \cdot kcal^{-1}}$) se sont traduits par l'AAC la plus faible parmi tous les régimes alimentaires essayés, ce qui indique une utilisation plus efficace des protéines contenues dans le régime alimentaire. Lorsque la teneur en lipides dans le régime alimentaire est de 23 %, une teneur en protéines inférieure à 34 % peut entraîner une réduction supplémentaire de l'AAC. Le laps de temps durant lequel le métabolisme était élevé après l'alimentation était indépendant de la teneur en protéines et en lipides du régime alimentaire, de même que de son apport énergétique. L'AAC chez la truite arc-en-ciel représentait l'équivalent de 15 à 24 % de l'apport énergétique des substances assimilables, suivant la composition du régime alimentaire. Une diminution des protéines dans le régime alimentaire et une augmentation simultanée des lipides dans la préparation d'aliments à des fins aquicoles pourrait améliorer la croissance en réduisant la dépense d'énergie utilisée pour l'AAC.

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A substantial loss of energy in the form of heat occurs after food is ingested by an animal. This increase in heat production, originally termed specific dynamic effect (Rubner 1902, cited in Kleiber 1975) and more recently specific dynamic action, calorigenic effect of food, or heat increment of feeding (Brody 1964), is the final result of many changes in intermediary metabolism; however, it is thought to result mainly from the deamination of ingested amino acids (Krebs 1964; Buttery and Annison 1973). Increased metabolic rate following feeding also results from energy expenditure associated with digestion, absorption, transportation, and deposition of food materials; this energy, while presumed to be minimal, is distinct from that for the heat increment, but difficult to separate experimentally. Where the distinction is not made, the term apparent heat increment (designated AHI hereafter) has been proposed (Beamish 1974).

The magnitude of the heat increment is dependent on the fate of food consumed by an animal. This in turn depends on the quantity, quality, and balance of dietary nutrients along with other environmental conditions. If the rate of ingestion of amino acids is greater than their rate of utilization in protein synthesis, excess amino acids are deaminated and the carbon residue either oxidized or stored as fat or carbohydrate (Cowey and Sargeant 1972). If the animal is fed poor quality proteins the rate of amino acid utilization in protein synthesis is restricted, resulting in an increased heat increment. Dietary protein is deaminated and oxidized if insufficient energy to fuel the body is available from other dietary components (Brody 1964). The addition of lipids or carbohydrates to such diets will "spare" the deamination and oxidation of dietary protein allowing its incorporation into body tissue (Forbes and Swift 1944). Provision of well-balanced diets at appropriate levels of intake can minimize waste energy liberated as a result of the heat increment and increase the efficiency with which food is utilized for growth.

The relatively few studies investigating the effect of diet composition on AHI of fish are conflicting. An elevation in AHI was suggested with an increase in protein level in nutritionally balanced diets fed to spontaneously active rainbow trout, *Salmo gairdneri* (Cho et al. 1976), and plaice, *Pleuronectes platessa* (Jobling and Davies 1980), but not in spontaneously active bluegill sunfish, *Lepomis macrochirus* (Schalles and Wissing 1976). Particularly little is known of the influence of the balance of dietary nutrients on AHI. A reduced AHI of protein was recorded when diets containing 25% carbohydrates were fed to largemouth bass, *Micropterus salmoides* (Tandler and Beamish 1980). Cho (1981) found that increasing the fat level in low-protein diets fed to groups of spontaneously active rainbow trout reduced the AHI.

In the present study, the magnitude of AHI was measured for rainbow trout fed diets with varying levels of protein and lipid. AHI of individual fish induced to maintain a steady level of activity was determined by indirect calorimetry. The main objective of the study was to determine the balance of dietary protein and lipid which resulted in the lowest AHI and therefore presumably the most efficient utilization of dietary protein.

Materials and Methods

Rainbow trout (5−10 g) were purchased from a private hatchery (Goossen's Trout Farm, Otterville, Ont.) and held in the laboratory in 340-L fiberglass-coated tanks supplied with aerated well water. Water chemistry was similar to that reported by Hodson and Sprague (1975). During holding, fish were fed a commercial trout diet (GRT-89G Martin Feed Mills, Elora, Ont.) to satiation once daily. Water temperature in the holding tanks was held at ≅11°C for a minimum of 2 wk and then increased $1°C \cdot d^{-1}$ to the experimental temperature of 15°C. Prior to use in an experiment, fish were held at 15°C for a period of 2 wk and then forced to swim for 1 wk against a current of $\cong 20\ cm \cdot s^{-1}$ ($\cong 2\ BL \cdot s^{-1}$) generated in an 80-L oval tank.

Measurements of oxygen uptake by rainbow trout were made between March and October 1983 in six modified Blazka-type respirometers (3.2 ± 0.1 L; Waiwood and Beamish 1978). Each chamber was supplied continuously with aerated well water (15 ± 0.1°C) at $\cong 2.4\ L \cdot h^{-1}$ in accordance with fish weight. Flow rate for an individual fish did not vary by more than $\pm 0.2\ L \cdot h^{-1}$. Respirometers were submerged in a temperature-controlled water bath to maintain the experimental temperature within the chambers. A curtain was kept around the water bath to minimize disturbance to the fish. Fish were continuously exposed to a light intensity of ≅60 lx to reduce diurnal fluctuations in metabolic rate (Hutchinson and Kohl 1971). Oxygen concentration of inflow and outflow water from each respirometer was measured by a probe (YSI model 54A) calibrated daily against an azide modification of the Winkler tritation method (APHA 1975). Oxygen concentration of inflow water remained constant at $\cong 9.4\ mg \cdot L^{-1}$, while that of the outflow never fell below $5\ mg \cdot L^{-1}$. The difference in oxygen concentration between inflow and outflow water was always at least $1\ mg \cdot L^{-1}$. Oxygen concentration of the inflow and outflow was measured and recorded for each chamber for 15 min of each hour over the entire experimental period. A characteristic of a continuous-flow system is a lag in response of oxygen concentration to a change in metabolic rate. To correct for this time lag, the hourly uptake of oxygen for each fish was calculated using the formula suggested by Fry (1971).

Individual fish (10−15 g) were weighed (±0.1 g), measured (±1.0 mm), and then placed in respirometers where they were forced to swim continuously against a current of $20\ cm \cdot s^{-1}$ ($\cong 2\ BL \cdot s^{-1}$). Fish always swam well within 24 h. The maximum cross-sectional area of the fish used in the experiments did not exceed 10% of the cross-sectional area of the swimming portion of the chambers. This ratio does not seriously affect the current velocity (Smit et al. 1971). The outer surface of the front portion of the chambers was darkened to encourage fish to maintain a constant position within the chambers.

At 17:00 on the third, fourth, and fifth day after introduction to the chambers, fish were fed a meal equal to 2% live body weight of a randomly assigned test diet through a vertical tube installed in the chamber. All fish consistently consumed the entire ration within 0.5 h. Following the three feedings, fish were deprived of food until their metabolic rate returned to the prefeeding level. Subsequently, at 17:00 on each of the following 2 d, fish were fed the same diet again at 2% initial live body weight. Oxygen uptake was monitored until it returned to the prefeeding level, at which time the fish were removed from the chambers and their weight (±0.1 g) and total length (±1.0 mm) again measured.

Oxygen uptake in respirometers was measured after fish were removed and attributed to an oxygen demand of organic material within the chamber. A linear increase in oxygen demand of the chamber from zero at the time of the first feeding to the final measured value was assumed. Oxygen demand of the respirometer was subtracted from the total measured oxygen uptake, the difference being attributed to oxygen uptake by the fish.

The increase in oxygen uptake above the prefeeding level was attributed to AHI of feeding. Fish were accustomed to a specific diet for 3 d. Oxygen uptake associated with the final 2 d of feeding was measured and converted to energy units using an oxycalorific coefficient of $3.42\ kcal \cdot mg\ O_2^{-1}$ (Brett and Groves 1979), halved, and equated to AHI per meal.

Twelve experimental diets were employed with protein levels of ≅34, 40, 48, and 60% and lipid levels of ≅7, 15, and 23% factorally combined (Table 1). Each test diet was fed to a total of five different fish.

Diet samples were freeze-dried to constant weight in a sublimator. Protein content was determined by the Kjeldahl method (Fels and Veatch 1959), protein being estimated from measurements of nitrogen multiplied by 6.25. Lipid analyses were performed using a Goldfisch fat extraction apparatus with chloroform−methanol (2:1 by volume) as the solvent (Folch et al. 1957). Gross energy content was determined in an adiabatic oxygen bomb calorimeter. All analyses were performed in duplicate. Digestible carbohydrate content of the test diets was calculated to be less than 2% of the total composition for all diets. Apparent digestible energy density was calculated by summation of the digestible energy of the individual components of the test diets (Cho et al. 1982).

Analysis of variance was performed to test for diet differences in AHI and duration of elevated metabolism following feeding. For AHI, regression of residuals from the analysis of variance on weight of food consumed by fish was significant ($p = 0.001$); therefore, adjustments were made by including this factor as a covariate. Time required for oxygen uptake to return to the prefeeding rate was found to be independent of weight of food consumed by fish over the range tested in this study. Analysis of variance including digestible energy intake as a covariate was performed to adjust AHI values to a common digestible energy intake. LSD multiple comparison procedures were used to compare means (Steele and Torrie 1960). Level of significance was $p < 0.05$ for all analyses. Values presented

TABLE 1. Composition of experimental test diets formulated by J. Hilton, Department of Nutrition, University of Guelph, Guelph, Ont.

Ingredient	Diet (% weight)											
	1	2	3	4	5	6	7	8	9	10	11	12
Fish meal (capelin, 68% C.P.)	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0
Soybean meal (48% C.P.)	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0
Gelatin	—	—	—	7.0	7.0	7.0	14.1	14.1	14.1	23.5	23.5	23.5
Wheat middlings (15% C.P., 8% fiber)	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Arginine	0.3	0.3	0.3	0.15	0.15	0.15	—	—	—	—	—	—
Methionine	0.5	0.5	0.5	0.45	0.45	0.45	0.4	0.4	0.4	0.25	0.25	0.25
Vitamin Premix[a]	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
Mineral Premix[a]	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Kaolin	18.8	15.3	11.8	15.3	11.8	8.3	11.8	8.3	4.8	7.1	3.6	—
Alpha floc	19.0	15.5	12.0	15.7	12.2	8.7	12.3	8.8	5.3	7.75	4.25	0.85
Fish oil (herring with antioxidant)	3.4	10.4	17.4	3.4	10.4	17.4	3.4	10.4	17.4	3.4	10.4	17.4
Composition												
Crude protein	34.2	34.2	34.3	40.8	39.3	41.3	48.0	48.2	48.7	60.1	58.7	58.5
Total lipid	6.9	15.1	24.0	8.1	15.6	23.4	7.3	15.3	22.5	6.4	13.6	21.1
Gross energy (kcal·g^{-1})	4.030	4.522	5.001	4.203	4.715	5.189	4.472	4.934	5.387	4.754	5.183	5.645
Digestible energy (kcal·g^{-1})	2.382	3.010	3.639	2.710	3.339	3.967	3.043	3.672	4.300	3.484	4.112	4.741
Protein to energy ratio (mg·kcal^{-1})	143.6	113.6	94.3	150.6	117.7	104.1	157.7	131.3	113.3	172.5	142.8	123.4

[a] Hilton and Slinger (1981).

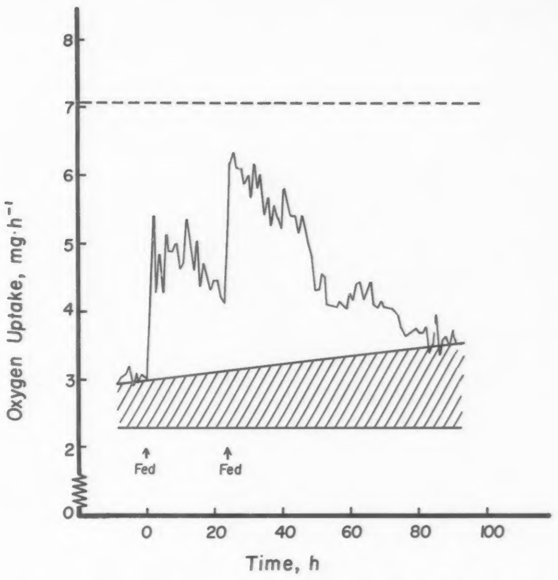

FIG. 1. Typical oxygen uptake curve for an individual fish (11.10 g) fed a meal equal to 2% live body weight on final 2 d of experimental period. Fish had previously been accustomed to the test diet for 3 d. Hatched area represents oxygen demand of respirometer. Broken line is calculated active rate of oxygen uptake.

parentheses following means in text and tables are standard errors of the mean.

Results

Oxygen uptake by rainbow trout increased abruptly following feeding, reaching a peak usually within 6 h (Fig. 1). Thereafter, oxygen uptake declined gradually until fish were fed again, 24 h after the first meal. At this time, oxygen uptake had not reached the prefeeding rate for fish fed any of the test diets. Following the second meal, oxygen uptake again increased abruptly, reaching a peak which was consistently higher than that following the first meal. Oxygen uptake then declined gradually until reaching the prefeeding rate, whereupon it stabilized. Most values for the peak rate of oxygen uptake following feeding were between 60 and 80% of the calculated active rate, and were never more than 95%. Active rate was calculated for each experimental fish according to its weight and the equation given by Rao (1969) for rainbow trout in freshwater at 15°C.

Time required for oxygen uptake to return to the prefeeding rate was not significantly influenced by apparent digestible energy intake of test diets, dietary protein, or lipid level. Overall mean time for oxygen uptake to return to prefeeding levels following the second meal was 58 ± 10 h (range 40−73 h).

Generally, AHI was positively related to apparent digestible energy of the test diet (Fig. 2). However, diets supplying 7 and 15% lipid appeared to have a "threshold" digestible energy intake, below which AHI did not decline with decreasing digestible energy of the test diet. The digestible energy intake per meal for test diets supplying 23% lipid appeared sufficiently high such that a "threshold" in the response was not observed. AHI did not differ significantly for diets 1 and 4, nor did it

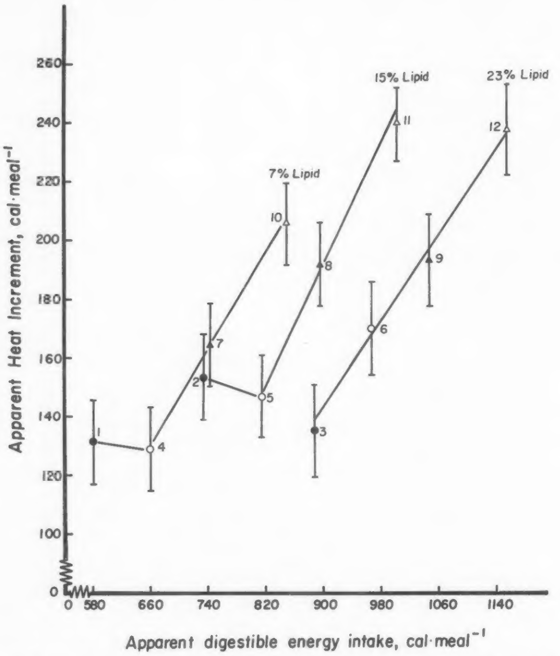

FIG. 2. Apparent heat increment in relation to apparent digestible energy intake of test diet. Closed and open circles represent 34 and 40% dietary protein, respectively. Closed and open triangles represent 48 and 60% dietary protein, respectively. Points represent a mean of five values except diets 3, 6, 9, and 12 where sample size is 4 and diet 11 where sample size is 6.

differ significantly for diets 2 and 5 (Fig. 2). Otherwise, for each dietary lipid level tested, an increase in dietary protein level, and therefore the total digestible energy intake, resulted in an increase in AHI. AHI and dietary lipid level were positively related for diets supplying 40% protein (Fig. 2). AHI for diets supplying 48 and 60% protein increased between 7 and 15% dietary lipid; however, a further increase in dietary lipid to 23% resulted in no further increase in AHI. Diets supplying 34% protein resulted in an increase in AHI between dietary lipid levels of 7 and 15%; however, a further increase in dietary lipid to 23% resulted in a decrease in AHI.

AHI adjusted to a common digestible energy intake (856 cal·meal⁻¹) for diets supplying 7 and 15% lipid was positively related to dietary protein level above 40% and negatively related to dietary protein level below 40% (Fig. 3). AHI adjusted for energy intake was not significantly different for diets supplying 7 and 15% lipid at any of the dietary protein levels tested. Mean AHI for diets supplying 23% lipid was significantly lower than diets supplying 7 or 15% lipid at all dietary protein levels tested except 40%. AHI for diets supplying 40% protein decreased with an increase in dietary lipid content, although not significantly.

AHI expressed relative to the digestible energy intake (Table 2) showed similar trends to AHI adjusted to a common digestible energy intake by analysis of covariance. Mean AHI for all dietary lipid levels tested relative to the apparent digestible energy intake decreased from 19.4 to 18.3% between 34 and 40% dietary protein. When dietary protein was increased from 40 to 60%, relative AHI rose from 18.3 to 23.0%. AHI relative to digestible energy intake averaged for all dietary protein levels tested was similar for diets supplying 7 and 15% lipid (22.0 and 21.1%, respectively) but decreased to 18.0% for diets supplying 23% lipid.

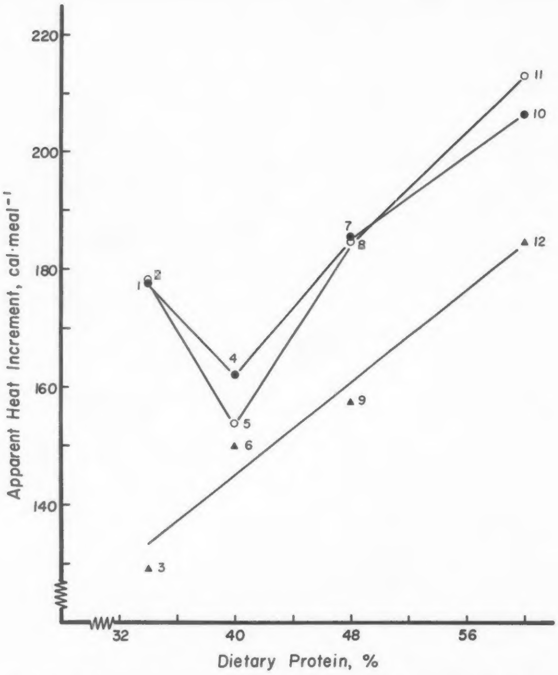

FIG. 3. Apparent heat increment adjusted to a common digestible energy intake (856 cal·d⁻¹), in relation to dietary protein and lipid level. Closed and open circles represent 7 and 15% dietary lipid, respectively. Closed triangles represent 23% dietary lipid. Points represent a mean of 5 values except diets 3, 6, 9, and 12 where sample size is 4 and diet 11 where sample size is 6.

TABLE 2. Comparison of apparent heat increment (AHI) values adjusted for digestible energy intake by analysis of covariance, and expressed relative to digestible and gross energy intake.

		AHI		
Diet	*n*	Adjusted by a linear component of covariate (digestible energy intake) (cal·meal⁻¹)	Relative to digestible energy intake (%)	Relative to gross energy intake (%)
1	5	177.5±20.4	22.4	13.2
2	5	178.2±14.5	20.7	13.7
3	4	129.4±16.3	15.2	11.1
4	5	161.9±18.0	19.2	12.4
5	5	153.8±14.6	18.2	12.9
6	4	150.2±16.5	17.6	13.4
7	5	185.1±15.4	22.2	15.1
8	5	184.6±14.9	21.4	15.9
9	4	157.7±18.8	18.5	14.8
10	5	206.7±14.4	24.0	17.6
11	6	212.9±14.7	24.1	19.2
12	4	184.6±20.9	20.8	17.3

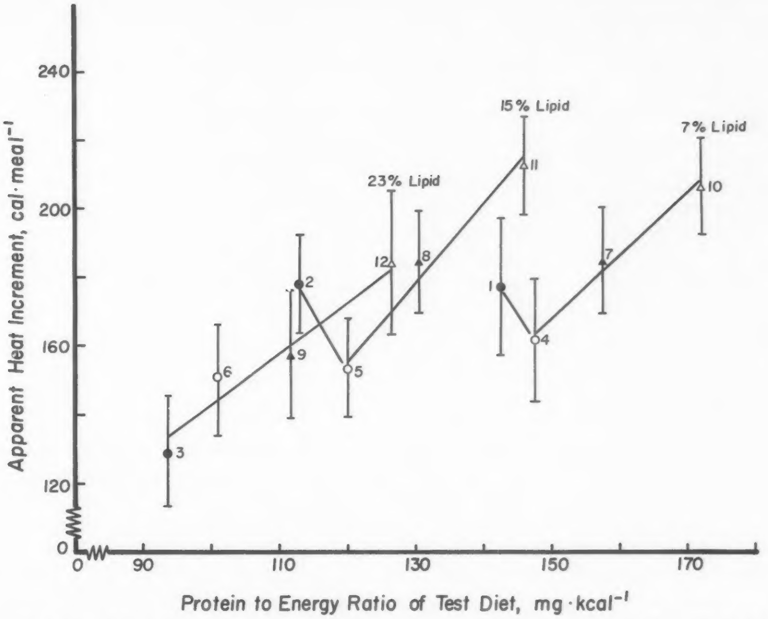

FIG. 4. Apparent heat increment adjusted to a common digestible energy intake (856 cal·d^{-1}), in relation to protein to energy ratio of test diet. Closed and open circles represent 34 and 40% dietary protein, respectively. Closed and open triangles represent 48 and 60% dietary protein, respectively. Points represent a mean of 5 values except diets 3, 6, 9, and 12 where sample size is 4 and diet 11 where sample size is 6.

Generally, AHI adjusted to a common digestible energy intake (856 cal·meal^{-1}) was positively related to the protein to energy ratio of the test diets (Fig. 4). Thus, AHI increased significantly from 129.4 ± 16.3 cal·meal^{-1} for diet 3 with a protein to energy ratio of 94.3 mg·kcal^{-1} to 212.9 ± 14.7 cal·meal^{-1} for diet 11 with a protein to energy ratio of 142.8 mg·kcal^{-1}. AHI adjusted to a common digestible energy intake for diets 1 and 2 was higher than predicted, given the protein to energy ratio of the test diets (Fig. 4). Otherwise, for each dietary lipid level tested, an increase in the protein to energy ratio of the test diet resulted in an increase in the AHI. The AHI for diets supplying 7% lipid appeared to be lower than predicted, given the protein to energy ratio of the test diets (Fig. 4).

Discussion

The present study has demonstrated that energy intake and diet composition influence AHI in rainbow trout. Differences in AHI attributable to diet can reflect the metabolic partition of dietary components between storage and catabolism as fuels. The need for energy favors catabolism of dietary components rather than incorporation into tissues. In the present study, AHI adjusted to a common digestible energy intake for high-lipid diets (23%) rose between 34 and 60% dietary protein. However, for low-lipid diets (7 and 15%), a decrease in dietary protein from 40 to 34% resulted in an increase in the AHI adjusted to a common digestible energy intake. These results suggest that at a "threshold" dietary energy intake, energy became limiting in low-protein (34%) , low-lipid (7 and 15%) diets, precluding the incorporation of dietary protein into tissue. Presumably in these cases, dietary protein was deaminated and oxidized for energy, resulting in an elevation of AHI. In support, Cho et al. (1976) found that lowering the protein level from 40 to 25% in diets fed to rainbow trout caused a reduction in energy retention and weight gain. Watanabe (1977) obtained relatively low values for protein efficiency ratio and net protein utilization when rainbow trout were fed low-protein diets containing 5% lipid. Thus, he similarly concluded that these diets supplied insufficient energy.

The rise in AHI with an elevation in dietary protein above 34% for high-lipid diets (23%) and above 40% for low-lipid diets (7 and 15%) is most likely due to increased deamination of excess amino acids. In accord, Cho et al. (1976) reported a decrease in protein retention by rainbow trout when dietary protein was raised from 40 to 60%. An increase in AHI with an elevation in dietary protein content has been reported for spontaneously active rainbow trout (Cho et al. 1976) and plaice (Jobling and Davies 1980). In contrast, Schalles and Wissing (1976) suggested that an increase from 24 to 45% in dietary protein did not affect the magnitude of the AHI of spontaneously active bluegill sunfish. They noted that AHI was highly variable among individual fish, however, and suggested that this may have obscured real differences among the diets.

The influence of increasing dietary lipid level on the AHI for a given energy intake in the present study was dependent on the dietary protein level. Numerous studies have demonstrated a protein sparing effect of increasing the lipid content of diets fed to rainbow trout (Lee and Putnam 1973; de la Higuera et al. 1977; Reinitz et al. 1978; Takeuchi et al. 1978a, 1978b; and others). The observed decrease in AHI for low-protein diets (34 and 40%) with an increase in dietary lipid from 7 to 23% is suggestive of such an effect. With increased dietary lipid available as an energy source, the amount of dietary protein deaminated and oxidized for energy in reduced, leaving more nitrogenous compounds available for growth. Evidence to support this was given by Lee and Putnam (1973) who recorded significantly lower growth rates for rainbow trout fed diets supplying 35% protein and 8 or 16% lipid as opposed to 24% dietary lipid.

A portion of dietary lipid appears to be deposited as tissue stores with little associated energy expenditure when high-protein (48 and 60%), high-lipid (23%) diets are fed to rainbow trout. In the present study, an increase in dietary lipid from 15 to 23% in high-protein diets (48 and 60%) did not result in a significant increase in absolute AHI, in spite of the high energy intake from the high-lipid diets. Cho et al. (1976) also found that the absolute AHI was similar for low-lipid (15%) and high-lipid diets (25%). Increasing the level of dietary lipid in high-protein diets fed to rainbow trout results in an increase in the amount of fat in the peritoneal cavity and viscera (Takeuchi et al. 1978a).

Diets supplying 34% protein and 23% lipid resulted in the lowest AHI of all diets tested, which indicates most efficient utilization of dietary protein. The absence of a "threshold" in the AHI for diets supplying 23% lipid, as was noted with diets supplying 7 and 15% lipid, suggests that for diets supplying 23% lipid, protein levels lower than 34% may result in a further reduction in AHI.

Generally, AHI adjusted to a common digestible energy intake was positively related to the protein to energy ratio of the test diet. This suggests an elevation in the amount of dietary protein deaminated with increasing protein to energy ratio of the test diet. In support of this suggestion, efficiency of dietary protein utilization in rainbow trout measured as gain per gram of protein ingested was shown to be negatively correlated with the protein to energy ratio of the diet (Lee and Putnam 1973). As well, Reinitz et al. (1978) found that protein retention in rainbow trout was negatively related to the protein to energy ratio of the test diet.

The results our study and those of Lee and Putnam (1973) suggests that diets supplying 34−35% protein and 23−24% lipid are optimal in terms of efficiency of utilization of dietary protein, although lower protein and higher lipid levels were not tested. Takeuchi et al. (1978a, 1978b) fed rainbow trout diets supplying 16−48% protein and 5−25% lipid and found that maximum protein retention occurred with diets containing 35% protein and ≅18% lipid.

Duration of elevated metabolism following feeding is highly variable among species of fish and under different experimental conditions. Reported values range from 8−18 h for thick-lipped mullet, *Crenimugil labrosus* (Flowerdew and Grove 1980), to 7 d for Atlantic cod, *Gadus morhua* (Saunders 1963). Biotic and abiotic factors affecting metabolism (Fry 1957) similarly influence the duration of elevated metabolism following feeding. Studies on different fishes indicate a positive correlation between duration of elevated metabolism and meal size (Beamish 1974; Vahl and Davenport 1979; Soofiani and Hawkins 1982), while fish weight and temperature are negatively related to duration of elevated metabolism (Saunders 1963; Beamish 1974; Tandler and Beamish 1980; Soofiani and Hawkins 1982).

Our results indicate that dietary protein level does not significantly influence the duration of elevated metabolism, which is consistent with Schalles and Wissing's (1976) data on spontaneously active bluegill. In contrast, elevated oxygen uptake by largemouth bass following feeding at high ratio levels has been correlated with time recorded for the absorption of protein (Beamish 1974).

AHI expressed relative to energy intake is useful for making general comparisons, or in constructing energy budgets of animals. However, unless the proportionate increase in AHI with increasing energy intake is measured, the effect is unknown, and statistical and graphic analyses are not valid (Atchley et al. 1976). The value of expressing data as a percentage of the energy intake is that it enables general comparisons to be made among species and diets. Values for AHI relative to the gross energy intake in rainbow trout were similar to those reported for other species fed natural and artificial diets with comparable protein levels. In our study, AHI for diets supplying 48 and 60% protein accounted for 15.3 and 1[illegible]% of the gross energy intake, respectively. Largemouth bass fed a diet of emerald shiners, *Notropis atherinoides*, consisting of 55% protein required the equivalent of 14.2% of the gross energy ingested for AHI (Beamish 1974). When fed a pelleted diet containing 50% protein, AHI of largemouth bass accounted for 15.8% of the gross energy intake (Tandler and Beamish 1980). Muir and Niimi (1972) reported AHI values of 16−19% of the gross ingested energy for two specimens of aholehole, *Kuhlia sandvicensis*, fed tuna flesh (≅65% protein).

Presentation of AHI relative to the gross energy intake is warranted if the objective is to construct a complete energy budget. However, since AHI is mainly a postabsorptive effect, variability due to differences in digestibility of diets can be eliminated by expressing AHI relative to digested energy.

AHI of trout relative to the digestible energy intake rose from 18.3 to 23.0% with an increase in dietary protein from 40 to 60%. Cho et al. (1976) reported an increase in AHI from 12.9 to 14.1% of the digestible energy intake associated with an elevation of dietary protein from 40 to 60% for spontaneously active trout. The lower values reported by Cho et al. (1976) may have been due to the inclusion of some energy associated with locomotory activity of fish in their measurements of AHI. Our study eliminated the cost of locomotion from the measurement of AHI, unlike many studies in which locomotory activity was neither controlled nor measured. Tandler and Beamish (1980) also reported an increase in relative AHI with an elevation in dietary protein content. In contrast, a relationship between relative AHI and dietary protein was not found for groups of rainbow trout forced to swim against a current (Medland and Beamish 1985).

AHI relative to digestible energy intake was similar for diets supplying 7 and 15% lipid (22.0 and 21.1%, respectively) but decreased to 18.0% with an elevation in dietary lipid to 23%. A similar absolute decline in AHI from 14.1 to 10.3% of the digestible energy intake was recorded by Cho et al. (1976) with an increase in dietary lipid from 15 to 25%. Medland and Beamish (1985) reported a decrease in AHI relative to digestible energy intake from 16.2 to 14.5% with an increase in dietary lipid from 7 to 23%.

AHI constitutes a substantial proportion of the total energy budget of a fish. In our study, it represented the equivalent of 15−24% of the digestible energy intake, depending on diet composition. Although seemingly wasteful, AHI is a necessary cost of food transformation. Careful attention to diet composition in formulating feeds for aquaculture purposes could enhance growth efficiency. Protein is usually the single most costly factor in the formulation of trout diets. If a diet contains an excess of protein in relation to the total amount of energy, protein is used as an energy source, rather than for growth.

Providing adequate energy with dietary lipids can minimize the use of more costly protein as an energy source, as well as reduce the energy expenditure associated with AHI.

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Sexual Differentiation and Use of Hormones to Control Sex in Yellow Perch (*Perca flavescens*)[1]

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Morphological and histologial studies demonstrated that estrogens and androgens affect sexual differentiation and can be used to control the phenotypic sex of yellow perch (*Perca flavescens*). Normal perch larvae of 5–10 mm total length (TL) had paired gonads with no sex-distinguishing features. In normal 16 mm TL perch, the gonads of females had fused into a single sac-shaped organ, while in males the gonads remained paired. Oogenesis had begun in most females of 35 mm TL. Spermatogenesis in males and vitellogenesis in females were first observed at 85 mm TL. Treatment (for 84 d) of perch (initially 20–35 mm TL) with estradiol-17β at 15–120 μg/g diet induced complete germ cell sex inversion in most males. Similar treatment with 17α-methyltestosterone at 1.5 to 60 μg/g diet induced spermatogenesis and the formation of ovotestes in females. Sperm collected from such ovotestes fertilized normal ova, and the resultant offspring were all female. Our findings indicate that in yellow perch: (1) differentiation of the somatic elements of the gonads precedes gametogenesis, (2) gametogenesis begins earlier in females than in males, (3) the attainment of a specific minimum body size (80–100 mm TL) is important to the initial onset of vitellogenesis and spermatogenesis, (4) both estrogens and androgens are probably involved in mediating sexual differentiation of germinal tissues, and (5) females are the homogametic sex.

Des études morphologiques et histologiques ont montré que les estrogènes et les androgènes influaient sur la différenciation sexuelle et pouvaient servir à déterminer le sexe phénotypique chez la perchaude (*Perca flavescens*). Des larves normales de perchaude de 5 à 10 mm de longueur totale (LT) présentaient des gonades appareillées sans caractéristique de différenciation sexuelle. Chez les perchaudes normales de LT de 16 mm, les gonades des femelles s'étaient fusionnées en un organe unique en forme de sac tandis que les gonades des mâles demeuraient appareillées. L'oogénèse avait débuté chez la plupart des femelles de 35 mm LT. La spermatogénèse chez les mâles et la vitellogénèse chez les femelles ont tout d'abord été observées chez des individus de 85 mm LT. L'administration (pendant 84 jours) à des perchaudes (LT initiale de 20–35 mm) d'estradiol-17β à raison de 15 à 120 μg/g de nourriture a provoqué une inversion sexuelle complète des cellules germinales chez la plupart des mâles. Un traitement semblable comportant l'administration de 17α-méthyltestostérone à raison de 1,5 à 60 μg/g de nourriture a provoqué la spermatogénèse et la formation d'ovotestis chez les femelles. Le sperme prélevé de ces ovotestis a permis de féconder des ovules normaux qui ont tous donné des femelles. Nos résultats obtenus chez la perchaude indiquent que : (1) la différenciation des éléments somatiques des gonades précède la gamétogénèse, (2) la gamétogénèse débute plus tôt chez les femelles que chez les mâles, (3) l'atteinte d'une taille minimale précise (80–100 mm LT) est importante pour l'amorce de la vitellogénèse et de la spermatogénèse, (4) les estrogènes et les androgènes jouent probablement un rôle de médiateurs de la différenciation sexuelle des tissus germinaux et (5) le sexe femelle est homogamétique.

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Administration of sex steroids before or during sexual differentiation has resulted in partial or complete sex inversion in various teleost fishes. Theses include the medaka (*Oryzias latipes*) and several tilapia (*Tilapia* or *Oreochromis* sp.) and salmonids (see Yamamoto 1969; Schreck 1974; Guerrero 1975; Donaldson and Hunter 1982; Hunter and Donaldson 1983). However, to our knowledge none of the mesothermal species classified as "coolwater" fishes (Kendall 1978) have been investigated in this regard.

Many economically important coolwater species, such as muskellunge (*Esox masquinongy*), walleye (*Stizostedion vitreum*), and yellow perch (*Perca flavescens*), exhibit sexually related dimorphic growth in which females grow faster and reach a larger ultimate size than males (Scott and Crossman 1973; Schott 1980). These differences have potentially important consequences for both the culture and management of these fishes. In studies on the feasibility of yellow perch aquaculture by our program, Schott et al. (1978) found that female perch raised in the laboratory grew significantly faster than males within the first year of life. Kocurek (1979) later confirmed this observation on fish reared under intensive culture conditions. The development of methods of controlling sex to produce all-female perch stocks would (1) increase the production potential of perch for commercial aquaculture and (2) have potential benefits to state and federal fish management agencies that rear closely related species (such as the walleye) for fishery enhancement (Schreiner 1984).

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Manipulation of sex by hormonal treatment requires an understanding of the timing of various stages of sexual differentiation. The timing of these stages is species specific and had not been previously described for perch. Accordingly, we first examined the normal morphological and histological development of perch gonads. Then we evaluated the effects of oral administration of estradiol-17β and 17α-methyltestosterone on the differentiation and development of perch gonads.

Materials and Methods

General Procedures

Methods of procuring and rearing yellow perch at our laboratory have been described (Malison et al. 1985). Production ponds were harvested, and perch were brought into the laboratory and trained to accept a commercial diet (Silver Cup salmon feed, Murray Elevators, Murray, UT 84107) when they were 20−35 mm total length (TL), 20 mm being the smallest size at which most fish (>80%) survive this transition (Best 1981). Except for experiments involving steroid treatments, fish were reared in 750-L round fiberglass tanks and fed to satiation at least twice daily. For all studies, water flow and aeration were adjusted to maintain good water quality and dissolved oxygen levels near saturation. Temperature and photoperiod were kept optimal for perch growth (21 ± 1°C, 16-h light : 8-h dark; see Huh et al. 1976).

Fish for histological study were killed by tricaine methanesulfonate (MS-222) overdose, measured (TL in millimetres), and placed in Bouin's fluid. Perch of 5−32 mm TL were left intact for paraffin embedding, and serial cross sections were taken from midbody to anus. The abdominal wall of fish larger than 25 mm TL was slit to facilitate fixation of gonadal tissues. Gonads from fish larger than 32 mm TL were removed prior to embedding and sectioning. Sections (6−8 μm) were cleared, stained with alum hemotoxylin and eosin, and permanently mounted and examined by light microscopy. Descriptions of gametogenesis in adult perch outlined by Turner (1919) and Malservisi and Magnin (1968) were used to identify stages of germ cell differentiation.

Normal Gonadal Differentiation

Normal differentiation of the gonads of larval and juvenile perch was studied both morphologically and histologically. Groups of five to eight perch each were sampled (sequentially over a 6-mo period) from a growing population as fish reached each of the following TL size ranges: 5−6, 8−10, 12−14, 16−18, 23−27, 35−40, 50−65, and 85−90 mm. Perch smaller than 20 mm TL were captured from rearing ponds at night using floating lights and a lift-net system developed by Manci et al. (1983). These fish were taken to the laboratory, held overnight in fiberglass tanks, and killed and examined the following morning. Perch larger than 20 mm TL were taken from rearing tanks in the laboratory.

Effects of Steroids on Gonadal Differentiation

For experiments on the effects of sex steroids, perch of 20−35 mm TL were harvested from rearing ponds and immediately weighed, measured, and randomly assigned to thirty 110-L round fiberglass tanks (61.0-cm diameter × 50.5-cm depth, with 2-L/min flow) at 30−35 fish per tank. Three tanks of fish were assigned to each treatment group. The fish in each tank were fed Silver Cup salmon feed to which one of the following dosages of steroids had been added: 17α-methyltestosterone (MT) at 1.5, 15, 30, or 60 μg/g diet; estradiol-17β (E_2) at 15, 30, 60, or 120 μg/g diet; or cholesterol (C) at 0 or 120 μg/g diet as a control. The method of preparing these diets has been described (Malison et al. 1985). Fish were fed experimental diets for 84 d and then fed untreated diet for an additional 35 d before most were sacrificed for morphological and histological examination.

Genotypic sex of all fish autopsied was determined on the basis of gonadal morphology (see Results). The gonadosomatic index (GSI = gonad weight·total body weight^{-1}·100) was calculated for three fish of each genotypic sex per tank, so that $N = 9$ fish per sex per treatment. These data were examined to determine treatment effects by analysis of variance followed by appropriate preplanned orthogonal comparisons.

Determination of Homogametic Sex

At the end of the experiment on hormonal sex control, some MT-treated fish were saved and transferred to outdoor tanks for overwintering under ambient environmental conditions (to insure normal sexual maturation, see Hokanson 1977; Kayes 1977). The following spring spawning season (April−May), these fish were killed and their gonads removed and examined. The gonads from four fish that were determined by gonadal morphology to be intersex genetic females (i.e. fish having a single gonad containing active spermatogenic tissue plus ovarian tissue) were teased apart in petri dishes, and the released sperm was used to fertilize eggs from wild adult female perch captured from Lake Mendota, Madison, WI. Four egg strands each fertilized by sperm from a different intersex genetic female were incubated in the normal manner (Malison et al. 1985). Two strands were later transferred to two separate rearing ponds. When the perch that hatched from these eggs reached 50−70 mm TL, 40 fish were removed from each pond and killed for sex determination and morphological and histological examination of the gonads.

Results

Normal Gonadal Differentiation

Histological inspection of the gonads of perch smaller than 16 mm TL revealed no sex-distinguishing characteristics. The indifferent gonads of 5−10 mm TL larval perch consisted of two separate strands of tissue situated dorsolateral to the intestine and in contact with the mesonephric tubules. These strands extended from about midgut to a point where they fused with the urogenital sinus near the anus. Germ cells measured 8−10 μm in diameter but could not be identified in every section from any one gonad. The gonads of 12−14 mm TL perch were flattened dorsolaterally (compared with the gonads of smaller fish) and were situated tangential to one another and

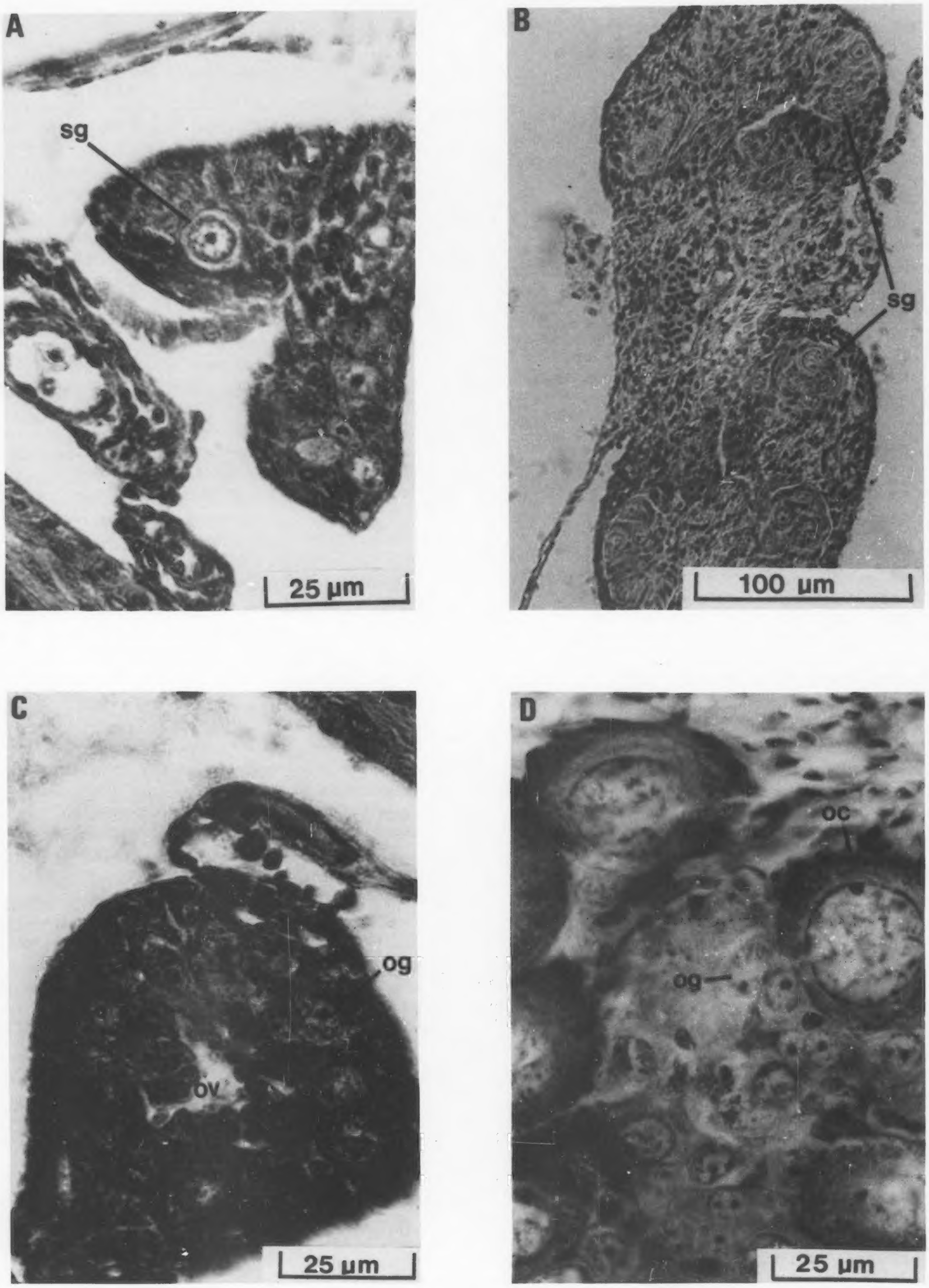
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FIG. 1. Cross sections of normal gonads from larval or juvenile yellow perch. (A) Testes from 18 mm (total length) male; (B) testes from 53 mm male; (C) ovary from 18 mm female; (D) ovary from 52 mm female. sg = spermatogonium, og = oogonium, ov = ovocoel, and oc = oocyte.

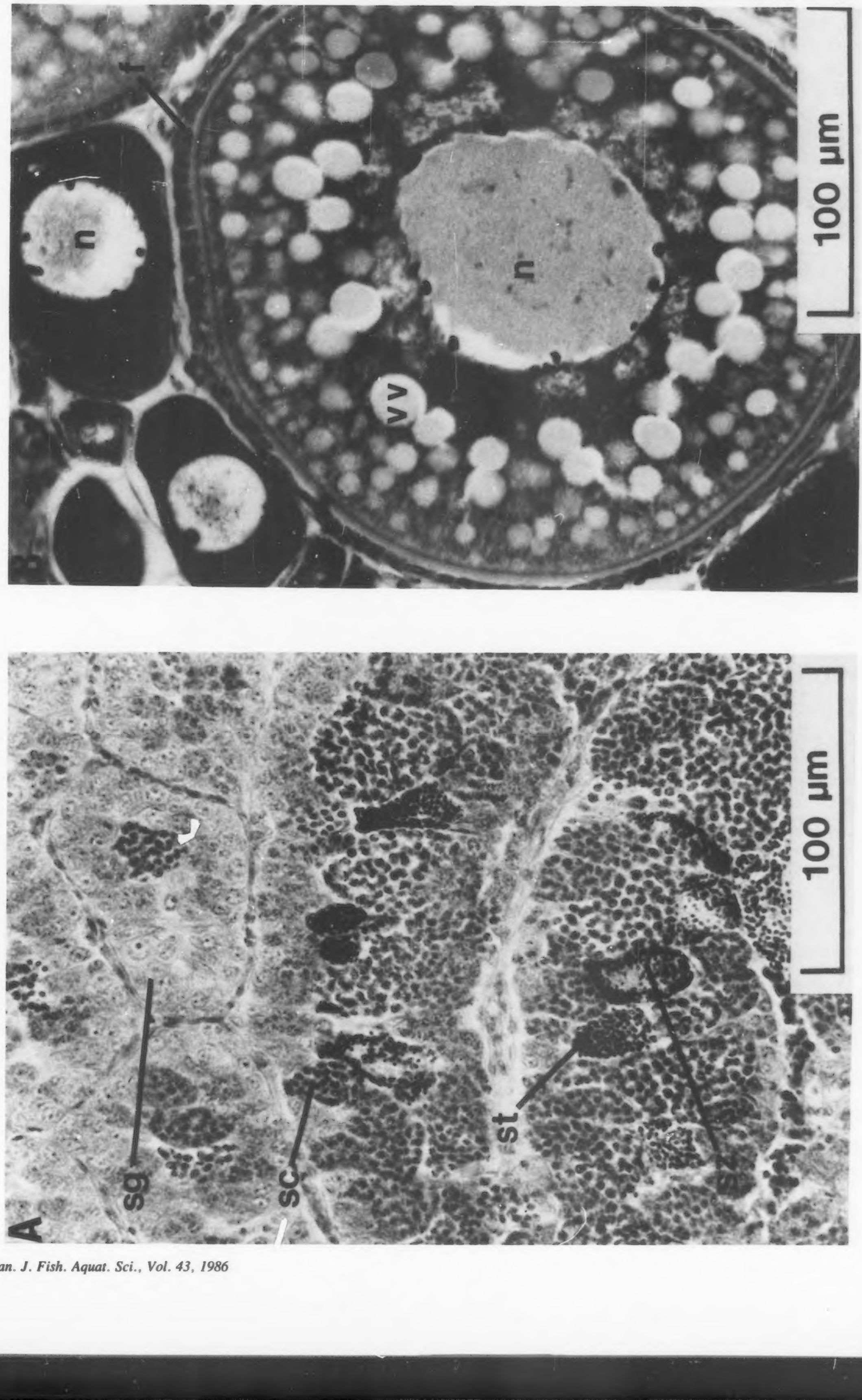


FIG. 2. Cross sections of normal gonads from juvenile yellow perch. (A) Spermatogenic testes from 87 mm (total length) male; (B) ovary with vitellogenic oocytes from 85 mm female. sg = spermatogonia, sc = spermatocytes, st = spermatids, sz = spermatozoa, vv = vitellous vacuole, n = nucleus, and f = follicle cells.

TABLE 1. Effects of steroid treatment on gonadal development in juvenile yellow perch.

Steroid and dose (µg/g diet)[a]	Percent distribution of gonad types per treatment group[b]				GSI ($x \pm$ SE)[c]
	Normal		Intersex or sex inverted		
	Paired testes	Single ovary	Single ovotestes	Paired ovary	
C 0	54.5	—	—	—	0.118±0.009
C 0	—	45.5	—	—	0.446±0.079
C 120	53.6	—	—	—	0.117±0.009
C 120	—	46.4	—	—	0.362±0.043
MT 1.5	53.2	—	—	—	0.182±0.043
MT 1.5	—	5.1	—	—	0.060±0.101
MT 1.5	—	—	41.7	—	0.120±0.024
MT 15	52.0	—	—	—	0.120±0.036
MT 15	—	1.3	—	—	0.014
MT 15	—	—	46.7	—	0.080±0.022
MT 30	50.6	—	—	—	0.084±0.020
MT 30	—	5.2	—	—	0.009±0.002
MT 30	—	—	44.2	—	0.028±0.007
MT 60	50.0	—	—	—	0.065±0.015
MT 60	—	5.7	—	—	0.026±0.008
MT 60	—	—	44.3	—	0.016±0.005
E_2 15	—	49.4	—	—	0.328±0.024
E_2 15	—	—	—	50.6	0.044±0.012
E_2 30	—	50.0	—	—	0.273±0.040
E_2 30	—	—	—	50.0	0.040±0.008
E_2 60	—	55.4	—	—	0.275±0.040
E_2 60	—	—	—	44.6	0.034±0.008
E_2 120	—	44.9	—	—	0.254±0.026
E_2 120	—	—	—	55.1	0.047±0.012

[a] Fish were fed diets to which one of three steroids were added: cholesterol (C) as a control, 17α-methyltestosterone (MT), or estradiol-17β (E_2).

[b] The percentage of fish in each treatment group ($N = 90-110$ fish per group) having each of the types of gonads indicated. Perch having ovotestes were considered genetic females; those with paired ovaries were considered genetic males.

[c] The gonadosomatic index (GSI) = gonad weight·total weight^{-1}·100. For each treatment group, $N = 18$ fish (9 for each genotypic sex). Orthogonal comparisons revealed the following differences ($P < 0.01$): C0 and C120 > (MT1.5 and MT15 > MT30 and MT60) for genetic females; MT1.5 and MT15 > MT30 and MT60 for genetic males; C0 and C120 > E_2 (all doses) for both sexes.

to the dorsal margin of the intestine. Development of the swim bladder had separated the mesonephros and gonads.

The sex of 16−18 mm TL perch could be distinguished by differences in shape of the gonads. The gonads of some fish of this size remained paired (or bilobed), whereas the gonads of others had fused to form a single structure (approximately oval in cross section) (see Fig. 1A and 1C). Perch of this size with a single gonad were considered female and those with paired gonads were considered male. This distinction was made because in larger perch, oogenesis was observed only in fish with single gonads, whereas spermatogenesis was seen only in fish with paired gonads. The ovary of 16−18 mm TL female perch was a sac-shaped structure 70−90 µm in diameter that contained a distinct internal cavity (ovocoel) lined with columnar epithelial cells. Each of the paired testes of male perch that were 16−18 mm TL was about 30 µm in diameter and contained no internal cavity. The protogonia observed in both types of gonads were identical in size (8−10 µm) and shape (round to oval).

In both male and female perch of 23−27 mm TL, the gonads were relatively larger than those of smaller fish. Histological examination revealed that the ovary was more bulbous and the ovocoel more prominent, and the paired nature of the testes was more distinct. Sex could be distinguished on the basis of gross morphology (i.e. single vs. paired gonad), without the use of a microscope. Germ cells in testes and ovaries remained similar to one another and did not differ in size from those of perch that were 18 mm TL.

Oocytes were first observed in the ovaries of female perch that were 35−40 mm TL. The largest oocytes in these fish were 20 µm in diameter and located in the anterior half of the ovary, while oogonia were more common in the posterior half. Ova-

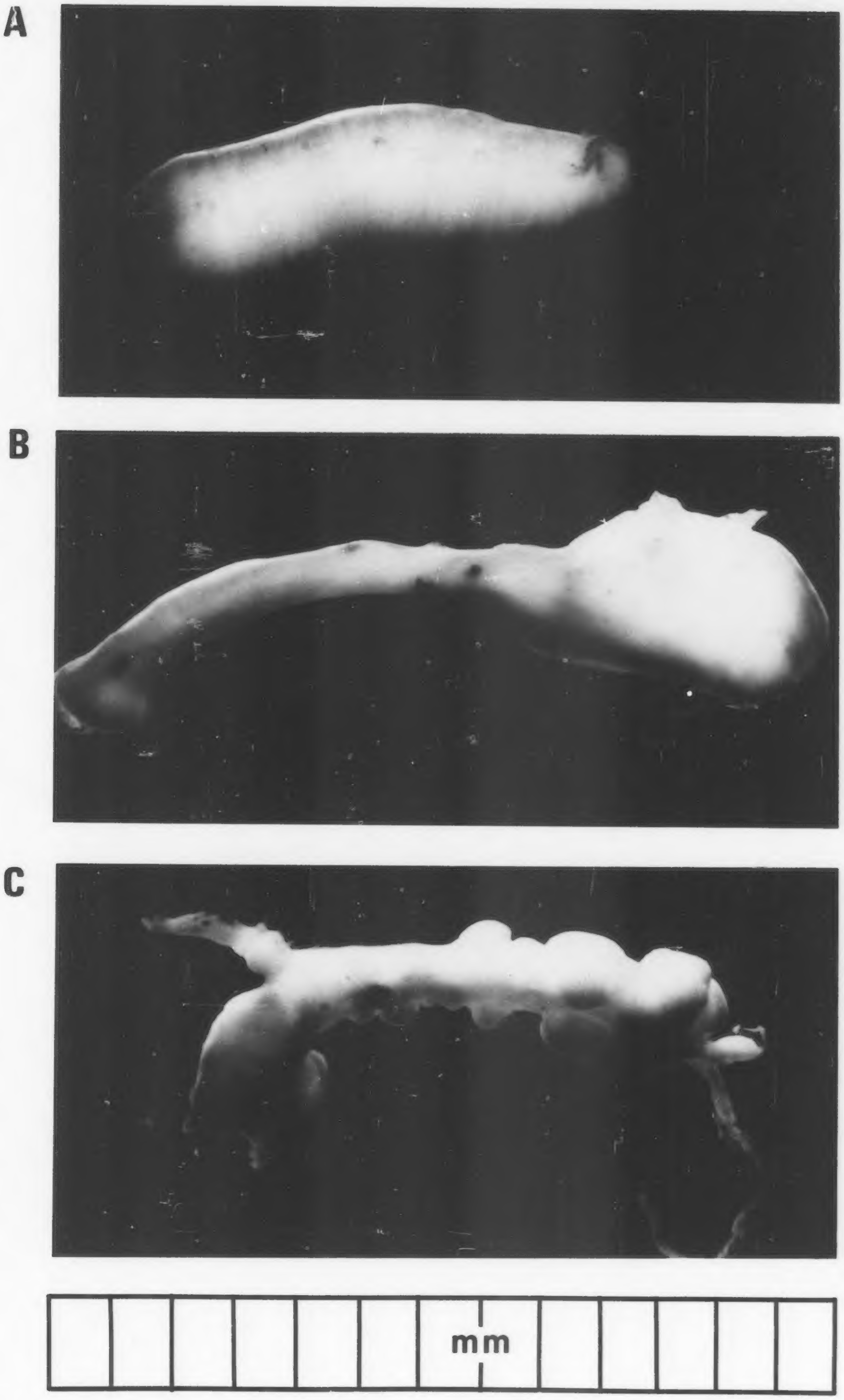


FIG. 3. Gross external morphology of gonads dissected from genetic female yellow perch. (A) Normal ovary from 101 mm (total length) female; (B and C) ovotestes from a 105 mm and a 98 mm female both treated with 17α-methyltestosterone. The posterior end of each gonad is to the right.

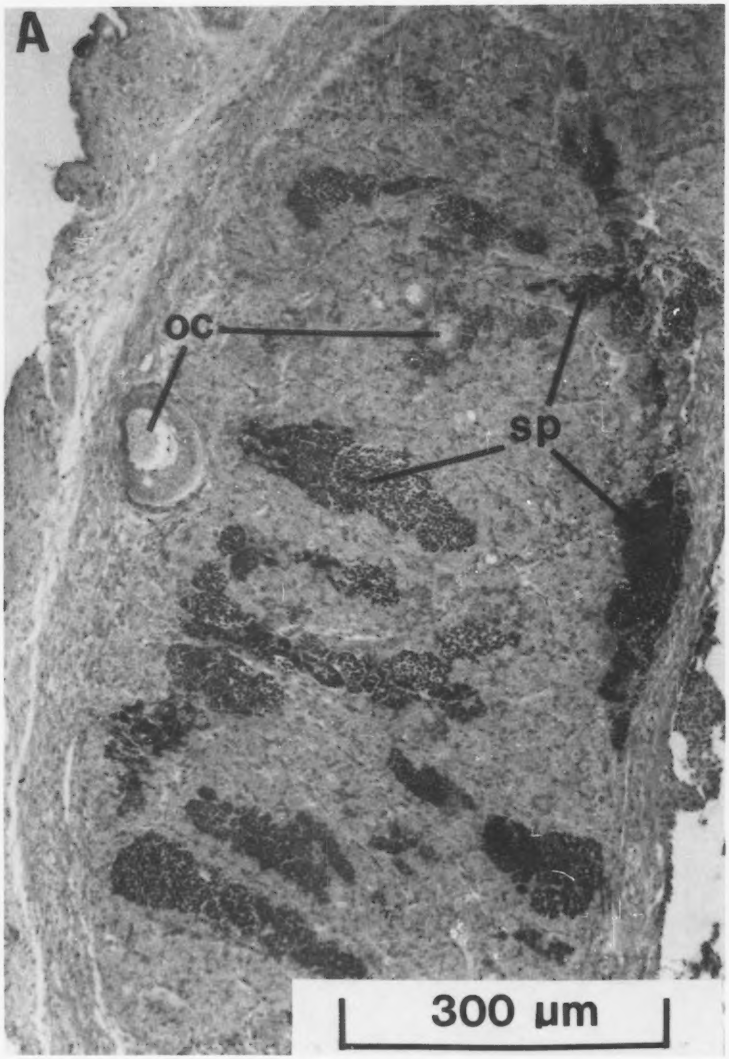
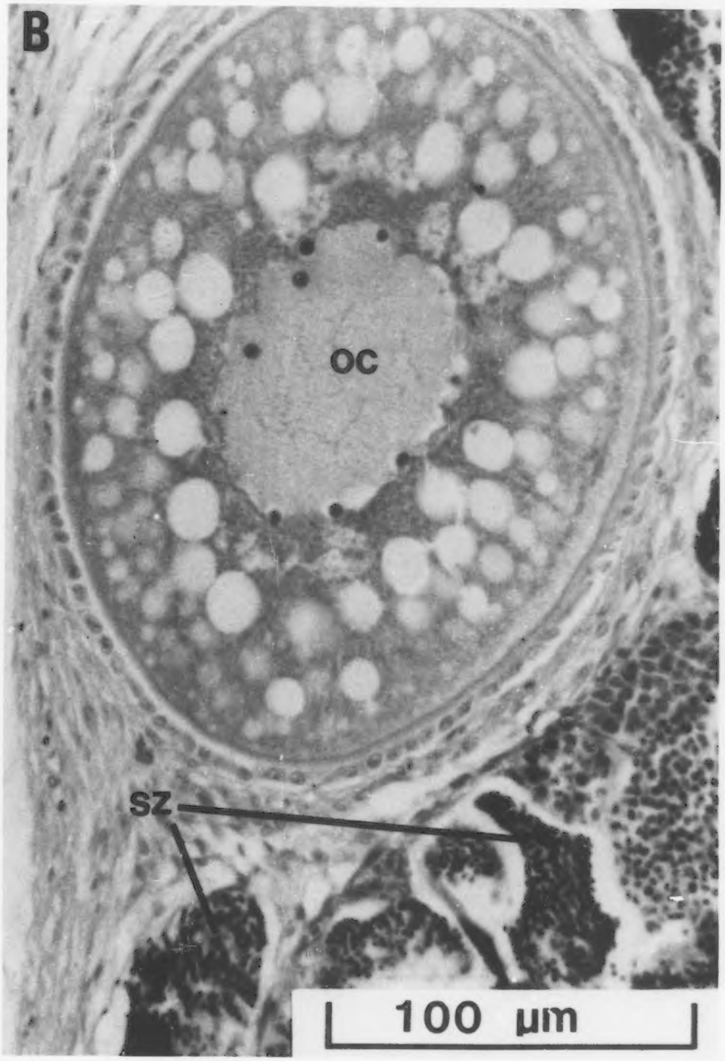


FIG. 4. Cross sections of ovotestes from genetic female yellow perch treated with 17α-methylte
matogenic tissue at various developmental stages, and sz = spermatozoa.


B
oc
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100 µm

ethyltestosterone. (A) 98 mm (total length) female; (B) 101 mm female. oc = oocyte, sp = sper-

ries were larger than testes and situated in the posterior quarter of the peritoneal cavity. No meiotic germ cells (spermatocytes, spermatids, or spermatozoa) were seen in the paired testes of 35–40 mm TL male perch. All spermatogonia were arranged in lobules. Testes remained smaller in diameter than ovaries but extended further anteriorly in the peritoneal cavity.

The germ cells in all males of 50–65 mm TL were similar to those in smaller perch. The diameter of each lobe of the paired testes had increased to 110–170 μm (Fig. 1B). Oocytes were common throughout the ovary of 50–65 mm TL females, and many of these oocytes were enlarged up to 30 μm (Fig. 1D).

Spermatocytes, spermatids, and spermatozoa were first detected in the testes of male perch that were 80–95 mm TL (Fig. 2A). However, the testes of several fish of this size contained only spermatogonia. Generally, germ cells within a given lobule were in a similar stage of development. The ovaries of 80–95 mm TL females contained many oocytes that were enlarged to about 250 μm in diameter. These oocytes contained many "vitellous vacuoles" (Malservisi and Magnin 1968) in the cytoplasm, and were completely surrounded by follicle cells (Fig. 2B).

Effects of Steroids on Gonadal Differentiation

The gonads of all perch fed cholesterol control diets appeared normal both morphologically and histologically. In contrast, the gonads of about half of the fish treated with either MT or E_2 had germinal tissues that were partially or completely sex inverted. As with untreated animals, steroid-treated fish with a single gonad were considered (genetic) females, and those with paired gonads were considered (genetic) males.

Three types of gonads were observed (Table 1) in the 90 MT-treated perch examined: (1) paired testes (51% of all MT-treated fish), (2) single ovaries (4% of all MT-treated fish), or (3) single gonads with abnormal morphology (45% of all MT-treated fish). Abnormalities in the latter were of two types: either the posterior half of the gonad was enlarged (Fig. 3B) compared with normal ovaries (Fig. 3A), or the gonad had one to several nodular outgrowths concentrated posteriorly (Fig. 3C). Histological examination revealed that the normal-appearing testes and ovaries resembled those of controls, while the abnormal gonads contained both oogenic and spermatogenic tissues (Fig. 4). Oocytes, some of which contained vitellous vacuoles and were surrounded by follicle cells, were present only in the medial anterior two-thirds of the abnormal gonads. The germinal tissue within the nodules or enlarged posterior half of these gonads contained spermatids and spermatozoa. The gonads that were enlarged posteriorly contained numerous large spaces (resembling the ovocoel of ovaries) separating the spermatogenic lobules. Because of these morphological and histological characteristics, all MT-treated fish with abnormal gonads (ovotestes) were classified as genetic females.

Of the 110 E_2-treated perch examined, 49.9% had gonads resembling the single ovaries of female controls. The gonads of the remaining E_2-treated animals were similar in gross morphology to the paired testes of control males. However, histological examination revealed that no spermatogenic tissue was present in these organs (Table 1). Most of the paired gonads of E_2-treated perch contained oocytes (Fig. 5), while the remainder appeared to be devoid of germ cells (sterile). None of the oocytes observed in these fish appeared to be vitellogenic. In contrast, many of the oocytes in control females and E_2-treated fish with single gonads were obviously vitellogenic. Based on morphology, all E_2-treated perch with paired gonads were classified as genetic males.

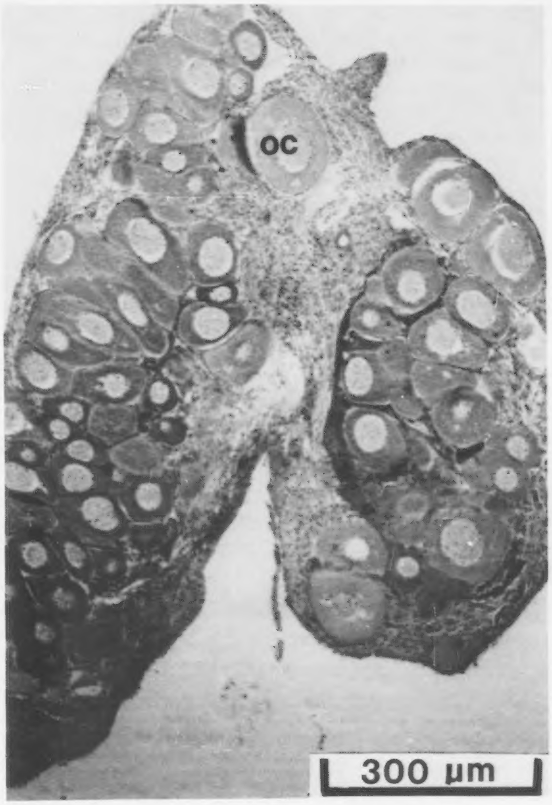

FIG. 5. Cross section of sex-inverted paired gonad from a 104 mm (total length) genetic male treated with estradiol-17β. oc = oocyte.

The GSI of genetic female perch treated with MT was lower than that of female controls (Table 1). The GSI of MT-treated fish of both sexes was inversely proportional to MT dosage. Both male and female perch treated with E_2 had lower GSI's than their respective controls.

Determination of Homogametic Sex

Several of the larger MT-treated perch that were overwintered had sperm in their gonads the following spring. The sperm collected from the ovotestes of four fish, determined to be intersex genetic females, fertilized (in each instance) normal perch eggs at a rate greater than 80%. The fertilized eggs and resultant fry developed and behaved normally. Subsequent morphological and histological examination of 40 offspring of each of two intersex genetic females revealed that 100% were normal females.

Discussion

We have described the process of sexual differentiation and development in yellow perch and demonstrated that steroids can be used to influence sex in this species. Our findings also indicate that, in both sexes of perch, sex-specific gonadogenesis (i.e. sexual differentiation of the somatic elements of the gonads) precedes the onset of gametogenesis. Takahashi (1975) observed a similar pattern in *Poecilia reticulata*. In perch, oogenesis in females began earlier (at a smaller body size) than spermatogenesis in males. Female perch are probably also the homogametic sex. These observations support Hunter and Donaldson's (1983) hypothesis that, in teleosts, germ cell differentiation does not necessarily begin first in the heterogametic sex, as has been suggested for mammals and birds (Hamilton 1965).

The initial onset of oogenesis, vitellogenesis, and spermatogenesis in perch does not appear to require changing environmental conditions. Similar results have been reported for other species, including brook trout (*Salvelinus fontinalis*) (Lam 1983). In our study, most female perch were probably in the laboratory under static environmental conditions prior to the onset of oogenesis, and certainly all were in the laboratory prior to the onset of vitellogenesis. In males, the earliest indications of spermatogenesis were observed well after fish had been moved into the laboratory.

Attainment of a minimum body size in perch seems to be a more important factor than either environmental cues or age in determining the initial onset of vitellogenesis and spermatogenesis. Vitellogenesis in females and spermatogenesis in males first became apparent in fish that were 85−90 mm TL (5−10 g total weight). Because these fish were kept under optimal growing conditions, they reached this size at 3−4 mo of age. We have also examined (unpublished data) the gonads of perch taken from several slower-growing populations, either from several northern Wisconsin lakes or reared in the laboratory in water too cold (10−11°C) to allow rapid growth. When examined, these fish were 55−65 mm TL, 1−2 g total weight, and 5−7 mo of age. Neither vitellogenesis nor spermatogenesis was apparent although these fish were 1−4 mo older than the fast-growing 85−90 mm TL perch (described earlier) that had signs of both vitellogenesis and spermatogenesis.

Attainment of a specific body size (80−100 mm TL and 5−10 g total weight) in perch may be important in determining the onset of physiological events besides vitellogenesis and spermatogenesis. Studies done in our laboratory (Schott et al. 1978) indicate that sexually related size dimorphism in perch can first be detected at 80−100 mm TL. The capacity of E_2 to stimulate growth also first becomes apparent at this size (Malison et al. 1985). All these physiological events may be linked to the maturation of certain endocrine mechanisms in the perch.

The treatment of 20−35 mm TL perch, with even very low levels of E_2 or MT, altered germ cell differentiation without changing certain morphological features, such as the single (for male) versus paired (for female) nature of the gonads. Male perch treated with E_2 exhibited no spermatogenic development, but females treated with MT had vitellogenic oocytes as well as spermatogenic tissues. Complete sex inversion (i.e. inversion of all somatic elements and morphological features of the gonad, and of 100% of the germ cells in females as well as males) possibly would have resulted had treatment been initiated in perch smaller than 16 mm TL (before the onset of sex-specific gonadogenesis). In experiments on sex inversion in coho salmon (*Oncorhynchus kisutch*), Goetz et al. (1979) examined the effects of dietary steroid treatment alone and in combination with steroid immersion of embryos and alevins. He reported greater success when the two procedures were combined. However, such investigations are currently impractical with perch, because perch smaller than 20 mm TL are difficult to train to commercial feeds and cannot be readily reared in the laboratory (Best 1981). At that size, sex-specific gonadogenesis has already begun. One practical advantage of initiating steroid treatment after the onset of sex-specific gonadogenesis is that the single versus paired nature of male and female gonads can be used to distinguish the genetic sex of treated perch.

Our studies provide evidence that ovarian development in the perch progresses from anterior to posterior. Similar observations have been made on *Poecilia reticulata* (Myamori 1961) and *Oryzias latipes* (Yamamoto 1958). In female perch controls, the most advanced oocytes were located in the anterior half of the ovary. In MT-treated females, oocytes were concentrated medially in the anterior two-thirds of the gonad, and spermatogenic tissues were concentrated posteriorly.

Sperm collected from (genetic) female perch treated with MT successfully fertilized normal eggs, and the resultant offspring were 100% female. These findings indicate that female perch are homogametic. In our opinion, the use of sperm from (partially or completely) sex-inverted genetic females is the method of choice for producing all-female stocks, because it is simple and effective and requires that only young fish destined to be broodstock be treated with steroids.

Patterns of sexual differentiation in other coolwater fish species probably resemble that in the yellow perch. Preliminary observations in our laboratory (unpublished) suggest that such is the case with walleye. If the above hypothesis is true, then methods similar to those we have described for perch could be used to manipulate sex in other coolwater species.

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Pathogenesis of Experimental *Edwardsiella ictaluri* Infections in Channel Catfish (*Ictalurus punctatus*)

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The lesions observed in channel catfish (*Ictalurus punctatus*) as a consequence of exposure to *Edwardsiella ictaluri* via gut and water were studied. Channel catfish fingerlings were exposed to 10^{10} bacterial cells via the gut and placed in tanks with unexposed fish. Both groups of fish were sampled periodically over a 35-day period. The gut-exposed fish exhibited gross signs of a systemic infection within 2 wk. Enteritis, hepatitis, interstitial nephritis, and myositis, all of which began as acute reactions and developed into chronic lesions, were observed histologically. Some of the contact fish developed systemic infections beginning in the intestine, thus demonstrating horizontal transmission. However, only contact fish developed the characteristic "hole in the head" lesion, which began in the olfactory sac and progressed to a granulomatous meningioencephalitis. These results indicate that both gut and nares are sites of primary infection in natural outbreaks of *E. ictaluri*.

On a étudié les lésions observées chez la barbue de rivière (*Ictalurus punctatus*) après qu'on eût exposé ce poisson à *Edwardsiella ictaluri* via l'intestin et l'eau. Des alevins de barbue de rivière ont été exposés à 10^{10} cellules bactériennes via l'intestin, puis placés dans des réservoirs en compagnie de poissons non exposés. Les deux groupes de poissons ont été échantillonnés périodiquement pendant 35 jours. Les poissons exposés aux bactéries via l'intestin ont montré en deux semaines des symptômes marcroscopiques d'infection généralisée. On a observé du point de vue histologique des cas d'entérite, d'hépatite, de néphrite interstitielle et de myosite qui ont tous commencé comme des réactions aiguës pour devenir des lésions chroniques. Des infections généralisées sont apparues à partir de l'intestin chez certains poissons mis en contact, ce qui indique qu'il y a eu transmission horizontale de l'infection. Cependant, la lésion caractéristique du « trou dans la tête », qui a commencé par une infection du sac olfactif et s'est transformée en une méningo-encéphalite granulomateuse, n'est apparue que chez les poissons mis en contact avec la bactérie. Ces résultats montrent que l'intestin et les narines sont les endroits d'infection primaire lors de manifestations naturelles d'*E. ictaluri*.

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In recent years, enteric septicemia of catfish (ESC) has become a major problem of intensively culture catfish. The disease was first described by Hawke (1979). The causative agent was later identified as *Edwardsiella ictaluri* (Hawke et al. 1981). Although this disease has increased in prevalence in the years since its description, very little information on routes of infection and pathogenesis is available. We undertook this study to determine natural routes of infection and to further elucidate the pathogenesis of the disease.

Areechon and Plumb (1983) studied the pathogenesis of *E. ictaluri* over a 6-d period in channel catfish (*Ictalurus punctatus*) fingerlings injected intraperitoneally with 2×10^4 bacterial cells. They observed anemia (normochromic, normocytic) and leucopenia in conjunction with necrosis of liver, spleen, and head kidney. A high number of *E. ictaluri* were present in these organs, reaching a maximum at 96 h and declining by the sixth day.

Similarly, using intraperitoneal injection, Plumb and Sanchez (1983) found that as few as 1.5×10^3 *E. ictaluri* would produce 100% mortality within 10 d. Mortality was shown to be dose related and *E. ictaluri* was consistently isolated from the liver, kidney, and peritoneal cavity of experimental fish. A separate experiment, in which 1.5×10^4 *E. ictaluri* were injected intraperitoneally into catfish, showed that the number of *E. ictaluri* in the liver decreased for 3 d and then increased logarithmically.

The pathological lesions associated with natural *E. ictaluri*

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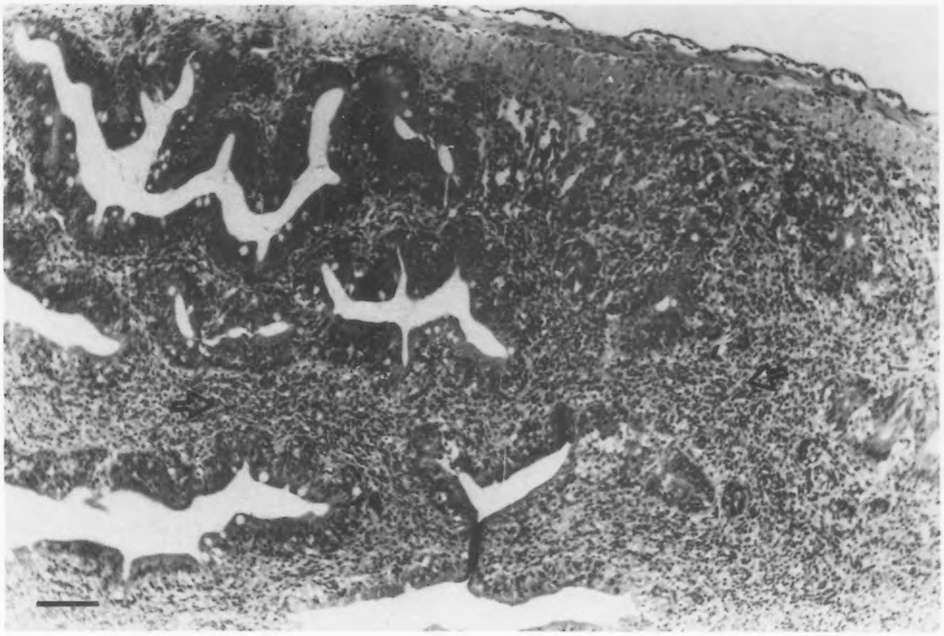

FIG. 1. Enteritis in a channel catfish 7 d after exposure to *E. ictaluri* via the gut. Proliferative reaction, composed primarily of macrophages with some neutrophils, is present throughout the submucosa (arrows) of the anterior intestine. H & E. Bar = 2 mm.

infections in both channel catfish and danios (*Danio devario*) have recently been described (Jarboe et al. 1984; Blazer et al. 1985). Infected catfish often have a characteristic "hole in the head" lesion which is an erosion of skin and muscle exposing underlying bone and occasionally the brain. In chronic cases, fish have a diffuse granulomatous enteritis, hepatitis, and meningioencephalitis. Brain lesions are generally confined to the telencephalon or olfactory lobe of the brain, olfactory bulb, and olfactory sac.

From histopathologic examination of infected fish, it appears that both nares and gut are possible routes of infection. Our research was initiated to determine whether one or both of these routes lead to systemic infections and/or death and to describe the pathogenesis of the disease in fish infected via both gut and nares.

Materials and Methods

For 2 wk, 150 *E. ictaluri* culture free fingerling channel catfish (8−10 g) were acclimated to 75.7-L tanks. The tanks were part of a 2271-L reuse system which had a sedimentation tank, biological filtration tank, and ultraviolet sterilization. Water temperature was 26 ± 1°C and the flow rate was 15 L/h. Fish were fed Purina catfish chow at a rate of 2−2.5% body weight/d.

Seventy-five fish were exposed via the gut. Each was lightly anesthetized with MS-222, the dorsal fin was clipped, and 0.5 mL of a 10^{10} *E. ictaluri*/mL suspension in phosphate-buffered saline was intubated into its stomach. This concentration of *E. ictaluri* represents a 24-h trypticase soy broth culture and was centrifuged prior to resuspension in an equal amount of saline. Plate counts were made of the suspension to determine the concentration of viable bacteria. Fifteen exposed and 15 unexposed (contact) fish were placed in each of five tanks and sampled over a 6-wk period. If present, moribund fish or fish with external lesions were killed at the time of sampling. Otherwise, fish were randomly sampled. Generally, three fish for histopathological evaluation and three fish for bacteriology were sacrificed each time. Fish for histopathology were fixed in 10% neutral buffered formalin. Bony tissues were decalcified in Kristenson's decalcifying solution. Tissues were routinely processed for histology, sectioned at 6 μm, and stained with hematoxylin and eosin.

The bacteriologic sampling procedure consisted of removing fish, anesthesizing them with MS-222, and then bleeding from the heart. The catfish were then killed and the brain, hind kidney, liver, stomach, and intestine were removed aceptically. The intestine was cut into fore- and hind-gut samples. Ten percent (wt/vol) tissue slurries were made by homogenizing samples in sterile saline. A blood sample was plated onto 5% bovine blood agar (BA) immediately after collection, and the remainder was inoculated into thioglycollate (thio) broth. The tissues were plated for quantitation onto BA and 1.0 mL of the slurry was added to thio broth. The BA plates were incubated at 30°C for at least 3 d and inspected each day for typical *E. ictaluri* colonies. After 48 h, routine bacterial transfers were made to screen for any atypical colonies. After 24 h at 30°C, the thio broths were plated onto BA (if negative they were blind transferred again after 5 d). The stomach and intestine samples were plated onto both BA and MacConkey (MAC) agar. Typical colonies were picked to triple sugar iron (TSI) agar and identified by standard methods (Buchanan and Gibbons 1974).

Water samples were taken daily for 2 wk to monitor the

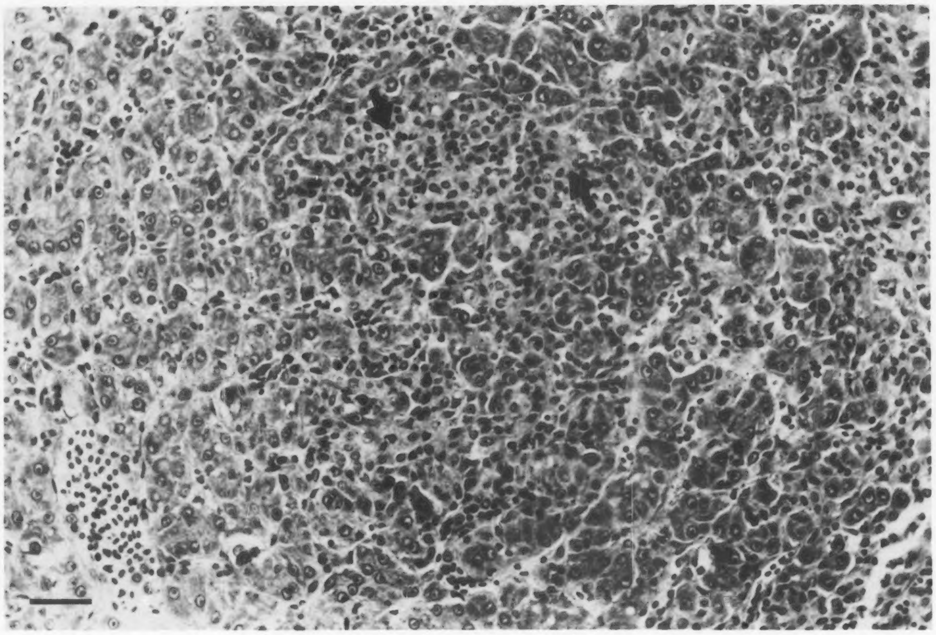

FIG. 2. Multifocal hepatitis in a channel catfish 2 wk after exposure to *E. ictaluri* via the gut. Accumulations of macrophages and neutrophils were observed throughout the liver (arrows). H & E. Bar = 0.5 mm.

E. ictaluri concentration. Samples were quantitatively plated for the recovery of *E. ictaluri*.

Results

Pathology of Gut-Exposed Fish

One of the three fish sampled at 24 h had an enteritis characterized by both granulocytic and mononuclear cells in the submucosa of the anterior intestine. By the third day postexposure, all fish examined had an inflammation of the anterior intestine, primarily in the submucosa. One fish had extensive pharyngitis and esophagitis involving both mucosa and submucosa. This may have been a consequence of mechanical injury during exposure. The majority of intestinal lesions were confined to the submucosa and muscularis. Involvement of the mucosa was rare.

By day 7, there was a proliferative enteritis in all fish examined (Fig. 1). At this time the reaction was primarily characterized by macrophages, and systemic infection was first apparent in the liver. Two fish had perivascular cuffing of neutrophils and the third had necrosis of hepatocytes with multifocal accumulations of macrophages and neutrophils (Fig. 2). One of the two with perivascular cuffing in the liver also had acute inflammation in loose connective tissue of the olfactory lamellae.

By 2 wk postexposure, many fish had gross signs of a systemic infection. Hemorrhagic lesions were apparent on the jaw and occasionally around the base of the fins. Internally, a bloody serous fluid was often present in the body cavity. An enlarged spleen as well as petechial hemorrhages in the liver, visceral fat, and intestine were common (Fig. 3). Histologically, lesions were found in the liver, kidney, spleen, intestine, and skeletal muscle. Lesions of the head kidney and interstitital tissue of the hind kidney were not consistent, but when present were small, multifocal accumulations of macrophages, many of which contained bacterial cells. All fish had multifocal accumulations of macrophages in the liver which also contained intracellular bacteria. In certain fish there was extensive necrosis of hepatocytes, especially around blood vessels and hence involving the hepatopancreas. The spleen was often congested, and the ellipsoids were very apparent. In some fish, cells of the arterial sheath were hypertrophied, vacuolated, and occasionally contained bacteria. The submucosa of the intestine contained a diffuse granulomatous reaction. Lesions of the skeletal muscle were primarily hemorrhages between the bundles. However, in the region of the jaw there was a mixed inflammatory response below the dermis and in some areas extending into the dermis. Neutrophils, macrophages, and lymphocytes were present.

Fish sampled on days 20 and 26 continued to have lesions consistent with a chronic systemic infection. In many fish the skeletal muscle lesions had progressed to a diffuse granulomatous reaction with some areas of granulation tissue apparent.

No exposed fish developed external head lesions or an infection of the olfactory bulb or telencephalon. A few fish did show involvement of the olfactory sac. This was manifested primarily as inflammation below the sensory epithelium. Occasionally, bacterial cells were observed within macrophages. One fish, sampled 25 d postexposure, had a diffuse granulomatous retinitis. Macrophages containing bacteria were evident. The reaction involved all layers of the retina and choroid body. The other eye had a mixed inflammatory reaction and edema of the cornea. This fish had a diffuse granulomatous myositis in the region of the jaw, and the liver contained focal accumulations of macrophages and neutrophils.

Also on day 26, one exposed fish had branchial hypertrophy and hyperplasia leading to fusion of the secondary lamellae. Macrophages containing bacteria were present.

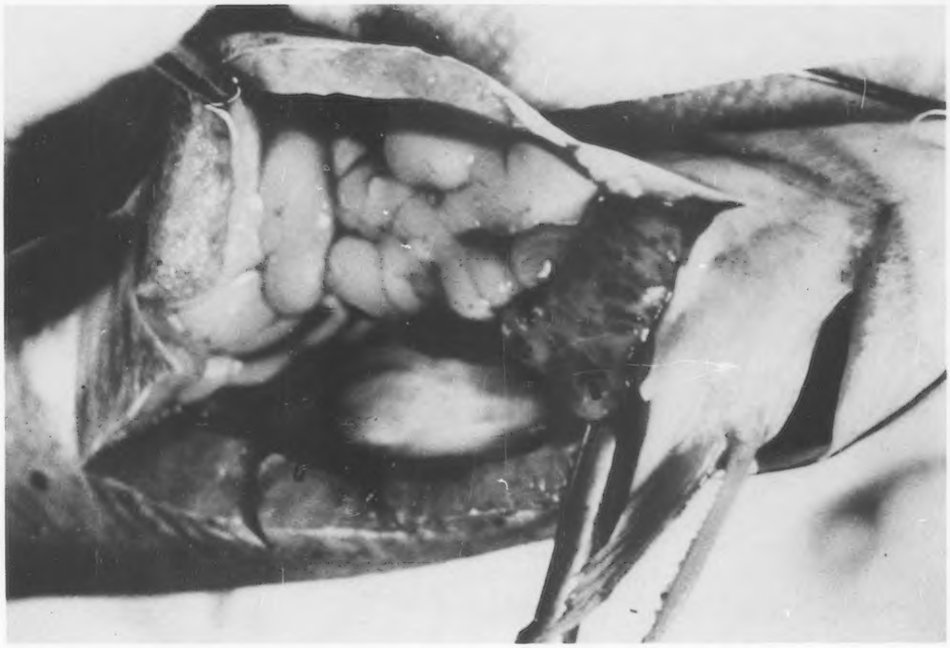

FIG. 3. Acute *E. ictaluri* infection in an channel catfish. Note congestion and hemorrhages in the liver (solid arrow) and bloody serous fluid within the body cavity (open arrow).

The exposed catfish were bacteriologically cultured 2, 5, 11, 26, 29, 35, and 120 d postexposure (DPE) (Table 1). All blood samples were negative. *Edwardsiella ictaluri* was only isolated from the brain of one fish on day 5. Kidney and liver samples were positive as early as 2 DPE and remained positive through day 26. The stomach, foregut, and hindgut were positive after 2 d, and became negative by the 11th DPE except for one fish which had a positive foregut and hindgut on day 29. After day 29, *E. ictaluri* was not isolated from any tissue.

TABLE 1. Recovery of *Edwardsiella ictaluri* from individual fish (no./g) following oral exposure.

Day	Brain	Kidney	Liver	Stomach	Foregut	Hindgut
2	0	<1 000	<1000	1000	2 000	0
	0	0	0	5000	100 000	1 000
5	7000	63 000	7000	0	0	0
	0	15 000	2000	0	0	0
	0	32 000	<1000	9000	2 000	126 000
11	0	1 000	3000	0	0	0
	0	<1 000	0	0	0	0
	0	2 000	1000	0	0	0
26	0	<1 000	2000	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
29	0	0	0	0	5 000	0
	0	0	0	0	0	0
	0	0	0	0	0	1 000
35	0	0	0	0	0	0
	0	0	0	0	0	0
120	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0

Pathology of Contact Fish

No lesions were observed in contact fish until the 16th day. Two of the three fish sampled at this time had lesions of the intestine and liver. There was an acute enteritis confined to the submucosa. Perivascular cuffing, foci or necrotic hepatocytes, and acute inflammation were present in the liver. One fish had a mixed inflammatory response in the loose connective tissue of the olfactory sac. A few granulocytes, lymphocytes, and macrophages, some of which contained bacteria, were present. Areas of inflammation (primarily macrophages containing bacteria) between and leading to fusion of olfactory lamellae were occasionally observed. Inflammatory cells surrounded the olfactory nerve and the periphery of the olfactory bulb (Fig. 4).

One fish on day 20 had a diffuse granulomatous reaction confined to the olfactory bulb. Numerous bacteria-laded macrophages were present. A second had inflammatory cells (neutrophils and macrophages) in the loose connective tissue of the olfactory sac. This fish had an enteritis restricted to the submucosa and a multifocal, acute heptitis.

Eight contact fish developed the external "hole in the head" lesion (Fig. 5), with the first observed 27 d after exposure to exposed fish. The external lesion was actually an erosion of skin and muscle overlying the telencephalon. Inflammation around the brain extended into and through the sutura fontanella to the exterior. Inflammation replaced skeletal muscle, dense connective tissue, and in one instance, actually invaded cartilage.

By the time the gross lesion was evident, a diffuse granulomatous response replaced most of the telencephalon or olfactory lobe of the brain. Numerous macrophages containing bacteria were apparent. In most fish the telencephalon was the only part of the brain (other than meninges) involved. In some fish an exudate, composed primarily of macrophages packed

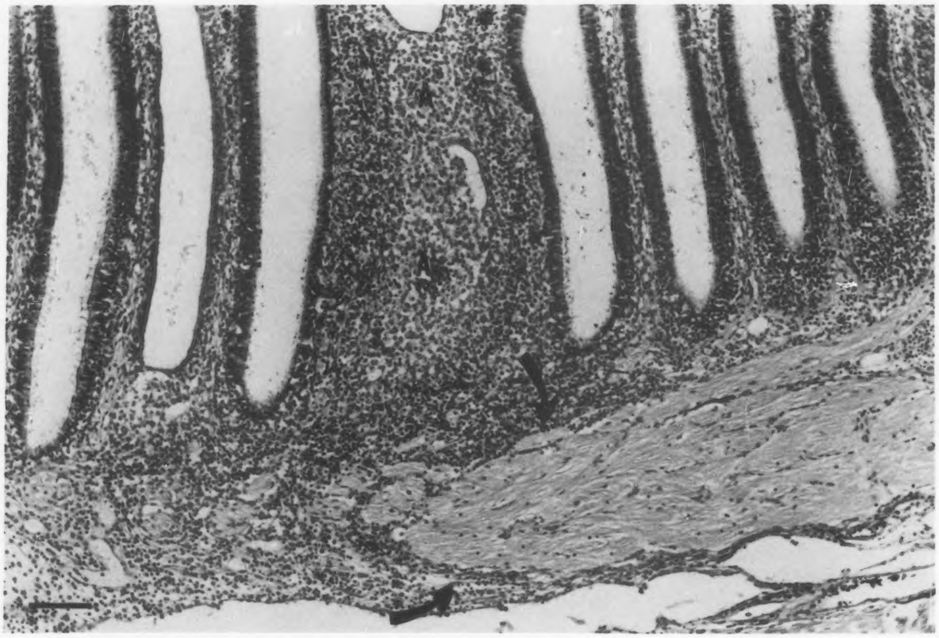

FIG. 4. Olfactory sac of a channel catfish 16 d after exposure to a gut-exposed fish. Chronic reaction, consisting primarily of macrophages containing bacteria, is present in the loose connective tissue of the sac, between the olfactory lamellae (A), and surrounding the olfactory nerve (arrows). H & E. Bar = 2 mm.

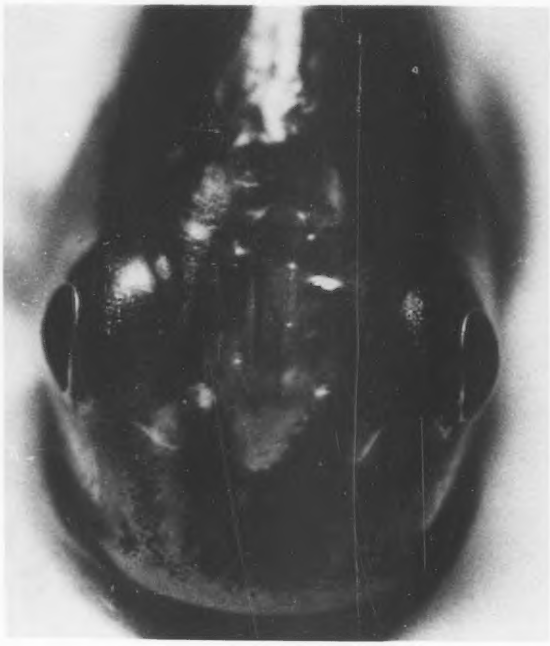

FIG. 5. Characteristic "hole in the head" lesion in a contact fish 27 d after exposure to gut-infected fish.

with bacteria, filled the ventricles. These macrophages were in various stages of degeneration. Occasionally the inflammation extended from the meninges into the periphery of other regions of the brain.

One fish had a systemic infection with involvement of liver, intestine, and kidney 35 d after contact with exposed fish. A second fish had a granulomatous inflammation of the olfactory bulb. The third fish had no significant lesions.

The contact catfish were bacteriologically cultured 7, 11, 16, 26, 29, 35, and 120 DPE (Table 2). All blood samples were negative. Two catfish with "hole in the head" lesions were cultured, one each on the 29th and 35th days, respectively; each had positive brain cultures (other "hole in the head" fish were used for histopathology). All other brain cultures of contact fish were negative. Only two kidney samples were culturally positive, at days 29 and 35. The liver was bacteriologically positive in one fish on the 16th DPE and again in a single fish on days 29 and 35. The stomach was culturally negative, but the foregut and hindgut were positive in one catfish on the 29th day. After the 35th day, *E. ictaluri* was not detected bacteriologically in any catfish.

From the 22nd to the 25th DPE, 14 catfish died; 12 of these were from the exposed group. These fish were not cultured due to the decomposed condition when found. No other deaths occurred.

Due to the design of this study, a total of 106 fish were removed for either bacterial or histopathologic study. This removal of fish complicates estimations of resulting mortality. Assuming that all fish showing histopathologic signs and all fish culturally positive for *E. ictaluri* would have died, the mortality from exposure is approximately 57% (43/75). The estimated mortality, using this reasoning, in the contact fish would be 2.5% (19/75).

Tank water was positive for *E. ictaluri* following introduction of the exposed fish at a level of 100/mL and decreased to 10/mL by the third day. *Edwardsiella ictaluri* concentration was 1/mL on the 7th DPE and was subsequently negative. Water cultures were continued through the 14th DPE before being discontinued.

Discussion

Fingerling channel catfish that were exposed to *E. ictaluri* via the gut began to show signs of a systemic infection within 2 wk. External lesions were grossly apparent and histologically the liver, spleen, kidney, intestine, and skeletal muscle were involved. The gross lesions — hemorrhages around the jaw, base of the fins and in the liver, visceral fat and intestines — are identical to those described in natural outbreaks (Hawke 1979).

In this study, mortality figures are difficult to obtain, since fish were collected for bacterial and histologic study from the experimental group. Since fish with gross lesions or moribund were used for these laboratory evaluations in preference to fish not showing signs, we would have to assume that they would have died. At the end of this experiment only 30 fish remained (10 exposed and 20 contacts). This would lead to an estimation of 41% mortality in the 150 fish studied. A further influence of mortality via feeding is evident in the early bacterial data which shows that the bulk of the inoculum was excreted. Similarly the relative numbers of bacteria noted in the brain of contact fish approximate the numbers found in the gut of exposed fish. While obviously serendipitous, this in some manner supports the large dose administered.

Histological lesions observed in the gut-exposed fish were also very similar to those described in natural outbreaks of pond-raised fish. In natural chronic infections, granulomatous hepatitis, enteritis, meningioencephalitis, and granulomatous inflammation with granulation tissue in the skeletal muscle of the jaw have all been described (Blazer et al. 1985). The only lesion we failed to reproduce in the gut-exposed fish was the brain lesion. This lesion was apparent in the contact fish, however.

Infections of the gut-exposed fish began in the intestine, spread first to the liver, and then to the spleen and kidney. The response during the acute phase (days 1−7) was mixed but was principally neutrophilic. During this time, intracellular bacteria were not observed. This is likely a reflection of the low phagocytic ability of catfish neutrophils. It is also possible that sufficient proliferation of bacteria for detection by histological means does not occur until later in the course of the infection. After 2 wk, the response was chronic, proliferative, and characterized by macrophages, many of which were packed with bacteria.

An important aspect of this disease needing further work is the role of macrophages. The presence of apparently viable bacteria within macrophages has been noted for *E. ictaluri* by Miyazaki and Plumb (1985) and for *E. tarda* by Kubota et al. (1982). In fish that succumb to *E. ictaluri*, the macrophage is apparently unable to eliminate the bacteria. Possibly the bacteria within the macrophages are viable (we believe they are) and they may actually proliferate within the macrophage.

Contact fish did not show signs of infection until 16 d after contact with gut-exposed fish. From 16 to 35 d after contact, fish were sampled that (1) showed signs of a systemic infection (gut and liver lesions) with no brain involvement, (2) had olfactory and brain lesions with no involvement of other organs, and (3) had olfactory and brain lesions as well as lesions of other organs. Tank water was positive for *E. ictaluri* through day 7 after contact and was negative until day 14, at which time sampling was discontinued. During chronic systemic infections (after 2 wk), fish may have begun shedding bacteria in numbers large enough to infect contact fish both via the gut and the nares. In a few cases, the gills may also be a route of infection. Infections via the gut lead to systemic infections and death. When infections occured via the nares, there was a progressive involvement of the olfactory sac, olfactory bulb, and telencephalon. Infections via the nares may or may not lead to systemic infections and ultimately death.

TABLE 2. Recovery of *Edwardsiella ictaluri* from individual fish (no./g) following water contact.

Day	Brain	Kidney	Liver	Stomach	Foregut	Hindgut
7	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
11	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
16	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	<1000	0	0	0
26	0	0	0	0	0	0
	0	0	0	0	0	0
29	0	0	0	0	0	0
	100 000	4 000	<1000	0	0	1000
35	70 000	35 000	4000	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0
120	0	0	0	0	0	0
	0	0	0	0	0	0
	0	0	0	0	0	0

None of the gut-exposed fish developed the external head lesion or brain lesions, despite the fact that some inflammation of the nares was observed. There are two possible explanations for this. First, fish that may have developed the brain lesions were killed before the infection was allowed to proceed to that point. Second, exposure via the gut may have stimulated the secretory immune system or nonspecific factors in mucosal surfaces. If the latter is true, previously exposed fish may be less susceptible to infection via the olfactory mucosa.

The natural disease seems to manifest itself in two forms: an acute gastrointestinal-septicemia with rapid mortality such as is seen with the exposed fish, and a "chronic" form characterized by the "hole in the head" lesion which may proceed secondarily into a septicemia and death. It appears from our findings that we have induced both forms of infection. Gastrointestinal exposure produced an acute septicemic form which was characterized by a rapid invasion and dissemination of the microorganism in the catfish. Bacteriologic findings in the intestine correlate with the enteritis seen on histopathology. Liver and kidney became culturally positive several days prior to histopathological changes, but histopathological findings continued to show evidence of chronic systemic infection after the fish were negative by culture. The mortality in these fish peaked at approximately the fourth week, when 12 deaths occurred.

The second form of the disease was produced in the contact fish resulting in characteristic lesions including "hole in the head." Bacteriological culture was consistent with histopathology, in that the fish having head lesions had cultural evidence of systemic infection. In our opinion it is significant that none of the orally exposed catfish produce a "hole in the head" lesion.

The absence of *E. ictaluri* from blood cultures might be explained in several ways. First, the time of sampling may not have coincided with periods of bacteremia. Second, the amount of blood cultured may have been inadequate (usually about 0.5 mL).

Bacteriologic examination of the tank water showed the presence of *E. ictaluri* in significant concentrations for 7 d, which might be anticipated when using an oral inoculation route. Culture of tank water was discontinued after 7 d of negative results. Plumb and Quinlan (1985) have noted the survival of *E. ictaluri* in pond water for 5 d at 5 and 25°C. However, they found that *E. ictaluri* could survive in pond bottom muds for at least 5 mo at 25°C. In retrospect, water should have been continuously sampled, especially during the third and fourth weeks of this study when the mortality peaked and shedding may have occurred.

From this study, we propose that the pathogenesis of enteric septicemia of catfish may occur in either of two forms. The first, an "acute form," follows the introduction of *E. ictaluri* into the gastrointestinal tract. This may occur when fish eat infected carcases or contaminated food, or possibly through the ingestion of contaminated water. The bacteria rapidly invade the intestinal lining and disseminate throughout the body. The route of dissemination is uncertain; preliminary evidence implicates fish macrophages as an important factor in this form. Macrophages containing bacteria were noted in every tissue examined. Death may occur rapidly and mortality appears to be dose dependent (Areechon and Plumb 1983). Brain involvement is not often noted in this form. A portion of these fish may recover and serve as shedders, excreting *E. ictaluri* into the water and thus infecting other fish.

The second or "chronic form" is often characterized by a classic "hole in the head" lesion. In this form of the disease, the fish initially are apparently infected via the nares. Contaminated water or mud may serve as a source of bacteria. The infection involves the olfactory bulb and appears to progress to the brain by direct extension of the bacterial infection along the olfactory nerve. The brain involvement seems to be localized in the telencephalon and meninges. The "hole in the head" lesion may follow establishment of chronic infection in the brain and subsequent production of "chondroitinase" by an in vivo microcolony of *E. ictaluri* (W. D. Waltman, E. B. Shotts, and T. C. Hsu, unpubl. data). This enzyme enhances the breakdown of the cartilagenous skull cap. This process may take 2–4 wk following initial infection. Catfish having brain involvement may survive for an undetermined period of time. At some point, by unknown means, the brain infection disseminates or secondary infection by other bacteria occurs, producing a septicemia and ultimately death.

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Uptake of Chrysotile Asbestos Fibers Alters Growth and Reproduction of Asiatic Clams

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Belanger, S. E., D. S. Cherry, and J. Cairns, Jr. 1986. Uptake of chrysotile asbestos fibers alters growth and reproduction of Asiatic clams. Can. J. Fish. Aquat. Sci. 43: 43–52.

The effects of chrysotile asbestos on siphoning activity, shell and tissue growth, fiber uptake, and gill ultrastructure in adult Asiatic clams (*Corbicula* sp.) and on larval release and mortality patterns from reproductively active adults were evaluated in 96-h to 30-d experiments at $0-10^8$ fibers/L. Adult siphoning activity was significantly ($\alpha = 0.05$) depressed in 96-h asbestos exposures when no food was offered or after 30 d when food was available. Shell growth was significantly inhibited in accordance with reduced siphoning. *Corbicula* exposed to 10^8 fibers/L accumulated 69.1 fibers/mg dry weight if food was offered. Fiber uptake was not observed at lower concentrations in 96-h or 30-d tests. Adult clams exposed to 10^8 fibers/L for 30 d accumulated 147.3 and 903.7 fibers/mg in gill and viscera, respectively. Gill tissue was significantly altered at 10^8 fibers/L and fibers were observed in gill locules and in ctenidial tissue. Fiber dimension analysis suggested that small, thin fibers were preferentially accumulated by both gill and visceral tissues. Significant increases in mortality of larvae exposed to asbestos and decreases in larvae released per milligram of adult dry weight were observed in reproductive adults exposed to asbestos at 10^4-10^8 fibers/L. *Corbicula* is an efficient accumulator of chrysotile asbestos and may be considered for use as an indicator of asbestos contamination.

On a évalué, au cours d'expériences d'une durée variant entre 96 h et 30 jours, et où la quantité de fibres variait de 0 à 10^8 fibres/L, les effets de l'asbeste chrysotile sur l'activité de siphonnement, la croissance des tissus et de la coquille, l'absorption de fibres et la structure fine de la branchie chez des clams asiatiques adultes (*Corbicula* sp.) ainsi que sur les modes de libération et de mortalité des larves venant d'adultes actifs sur le plan de la reproduction. L'activité de siphonnement des adultes a été sensiblement réduite ($\alpha = 0{,}05$) chez les individus exposés à l'asbeste pendant 96 h lorsqu'on ne donnait aucune nourriture ou après 30 jours lorsque de la nourriture était disponible. On a noté une diminution importante de la croissance de la coquille correspondant à une réduction de l'activité de siphonnement. Les *Corbicula* exposés à une concentration de 10^8 fibres/L ont accumulé 69,1 fibres/mg de poids sec lorsqu'on leur donnait de la nourriture. On n'a pas observé d'absorption de fibres à des concentrations plus faibles dans les essais de 96 h ou de 30 jours. Les clams adultes exposés à une concentration de 10^8 fibres/L pendant 30 jours ont accumulé respectivement dans la branchie et les viscères 147,3 et 903,7 fibres/mg. Le tissu branchial a été sensiblement altéré lorsque la teneur en fibres était de 10^8/L et l'on a observé la présence de fibres dans les loges branchiales et dans le tissu des cténidies. L'analyse de la dimension des fibres semble indiquer que les fibres minces et petites s'accumulent de préférence dans les tissus viscéral et branchial. On a observé chez les adultes reproducteurs exposés à l'asbeste dont les concentrations variaient de 10^4 à 10^8 fibres/L une augmentation importante de la mortalité des larves qui avaient été exposées et une diminution des larves libérées/mg de poids sec des adultes. *Corbicula* accumule de façon efficace l'asbeste chrysotile et peut servir d'indicateur de la contamination par l'asbeste.

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Asbestos is a generic term for a group of intergrading hydrated silicate minerals with the fibers having an aspect ratio (length/width) of 3 to 1 or greater (Speil and Leineweber 1969). Mineralogically, asbestos occurs in two major forms, serpentine chrysotile and amphibole. Chrysotile accounts for 95% of the asbestos used industrially as an insulation material, fire retardant, and strengthening agent (Levine 1978).

Distribution of asbestos in water, particularly chrysotile, is known worldwide (Millette et al. 1980; Spurny and Schörmann 1983), and particle concentrations in excess of 10^6 fibers/L are common. In a survey of 406 separate water supplies in the United States, Millette et al. (1980) found that nearly 20% had greater than 10^6 fibers/L. Release of asbestos into water occurs via mining of asbestos (Cunningham and Pontefract 1971; Hayward 1984) and other minerals such as iron ore (Cook et al. 1974) and nickel (Langer et al. 1980), use of asbestos-containing materials (Puffer et al. 1980; Williams and Muhlbaier 1982), deposition of atmospherically suspended fibers (Hesse and Hallenbeck 1978; Mizota 1982), and erosion of serpentine chrysotile parent rock (McGuire et al. 1982; Hayward 1984).

Asbestos has been implicated as a potent carcinogenic and toxicologic agent in mammals. Cook and Olson (1979) reported that amphibole asbestos was eliminated via urine in human subjects who drank asbestos-tainted water. Epidemiological studies of excess cancer risk in populations using asbestos-contaminated waters as a drinking water source have been inconclusive. Some studies (Sigurdson et al. 1981; Polissar et al. 1982) failed to link asbestos to increased risks of cancer, while others (Kanarek et al. 1980; Graham 1981) correlated asbestos to elevated risks of pancreatic, stomach, esophogeal, and mesothelioma cancers.

The impact of asbestos on aquatic life has been largely ignored. Halsband (1974) exposed mussels (*Mytilus* sp.) to high concentrations of chrysotile (1−100 mg/L) for 10 d which resulted in accumulations of fibers and asbestos blocks in intestinal lining tissue. Fibers were not displaced when mussels were replaced in clean water. Batterman and Cook (1981) determined chrysotile burdens in salmonids from Lake Superior and Hudson Bay that had histories of exposure to asbestos. Arctic char (*Salvelinus alpinus*) from Deception Bay, Canada (an arm of Hudson Bay), had 2.9 and 230.5 fibers/mg in muscle and kidney tissue, respectively, while the Bay had fiber concentrations as high as 6.7×10^8 fibers/L. Woodhead et al. (1983) exposed mollies (*Poecilia formosa*) for 6 mo to chrysotile and found that fish developed epithelial hypertrophy, selective necrosis in kidney cells, and vacuolation in heart cells. Belanger et al. (1985) found that effects of chrysotile on larval coho salmon (*Oncorhynchus kisutch*) exposed from 40 to 80 d at 10^6 fibers/L included lethargic behavior, epidermal hypertrophy, hyperplasia and selective vacuolation near the branchial region, and degradation of the lateral line system. Ecopathological studies on the effects of asbestos in aquatic organisms have not been performed in a systematic fashion, but Black et al. (1982) described mesothelioma in walleye (*Stizostedion vitreum*) in Torch Lake, Michigan, exposed to copper tailings probably containing asbestos. Mesothelioma neoplastic lesions are a peculiar carcinoma that is strongly associated with asbestos exposure in mammals (Selikoff and Lee 1978; Triol et al. 1984). Evidence for concern clearly exists for aquatically transmitted asbestos.

This study evaluates short-term (96 h) and long-term (30 d) effects of chrysotile to the Asiatic clam, *Corbicula* sp. The exact taxonomic status of the Asiatic clam introduced to the United States in the 1920s (McMahon 1982) is not clearly understood (Hillis and Patton 1982). Britton and Morton (1979) originally declared the species to be *Corbicula fluminea* (Müller 1774). Prior to this the clam also appeared in the literature as *Corbicula manilensis*. The *Corbicula* evaluated in this study conforms to the white form (white nacre) of Hillis and Patton (1982).

Mortality, tissue and shell growth, siphoning behavior, gill tissue pathology, and fiber uptake were assessed for 30-d exposures in the laboratory. Larval clam mortality and release patterns from reproductive adults were assessed in 14-d exposures and mortality, fiber uptake, and siphoning behavior in 96-h exposures. Mortality was considered to be an unlikely contributor to the analysis of the effects of asbestos on clams because previous researchers (Halsband 1974; Woodhead et al. 1983; Belanger et al. 1985) found acute mortality to be insignificant for adult mollusks and a variety of fish species. Siphoning behavior and growth of *Corbicula* are intimately related and are of considerable ecological and toxicological importance (Haines 1979; Foe and Knight 1985a). Pathologies associated with asbestos exposure are diverse and reflect subtle stress effects. In this study, gill tissue ultrastructure was evaluated, since delicate gill tissues would represent one major route of fiber accumulation. Uptake of chrysotile fibers in gill and visceral tissues was determined by transmission electron microscopy (TEM), and we have integrated these observations to our findings on growth and siphoning behavior. Release of larvae by reproductively active adults and larval mortality were investigated at different levels of asbestos exposure. Release of gill incubated veligers was used to corroborate siphoning behavior observations, since release would be coincident with the amount of time that the valves were parted.

Materials and Methods

Corbicula Collection and Handling

We selected *Corbicula* for these studies for four reasons: (1) it resides in every major river system in the United States (McMahon 1982) and, therefore, is likely to be found within several chrysotile-contaminated waterways; (2) mollusks are known to accumulate asbestos; (3) clams are easy to collect and observe in laboratory environments; and (4) known effects of other toxicants on clams allow comparisons.

Adult *Corbicula*, 12.5- to 17.0-mm shell length, were collected by dip net from the New River, Virginia, and transported to Virginia Tech. Clams were held in 40-L aquaria for 7−14 d for acclimation to laboratory conditions and fed *Chlamydomonas reinhardti* cultured in Bold's basic medium (Carolina Biological Supply 1978). Algae were added daily to the aquaria to achieve a final algal density of 10^6 cells/L.

Chrysotile Determinations and Preparations

We obtained grade-5 chrysotile mined ore from a commercial supplier, and suspensions were prepared by lightly milling 400 mg of asbestos, followed by sonicating 500 mL of a 0.060 mg chrysotile/L stock for 2 h using a Fisher Ultrasonic Cleaner. Five replicate determinations of the fiber concentrations indicated that the actual concentration would lie between 2.5×10^8 and 8.8×10^9 fibers/L.

Fiber identification and determinations were made by the methods outlined by Anderson and Long (1980). Water samples were collected in asbestos-free nalgene bottles and filtered through 0.2-μm-pore polycarbonate filters. The samples then were carbon coated, inverted, and placed in a Jaffe-Wick washer for 36 h on brass TEM grids saturated with chloroform. Fiber density estimates were derived by counting three replicate grids of 5−10 grid holes per grid (a total of 15−30 holes). Background (i.e. control) and blanks were processed simultaneously. Fibers were identified by the characteristic transmission pattern of a central canal and sheath appearance (Fig. 1) using a JEOL JEM 100C transmission electron microscope. Time constraints limited the number of fiber concentration determinations that we could make. Individual analyses, from sample collection to concentration determination by TEM, required ~2 d for water and 3.5 d for tissue samples. Therefore, water samples from three 96-h and two to five 30-d experiments were pooled for analysis of realized and nominal concentrations. Actual fiber densities for control, 10^4, 10^5, 10^6, and 10^8 fibers/L (Mean ± SE) were 0 ($n = 6$), 0 ($n = 3$), $1.9 \pm 0.7 \times 10^5$ ($n = 5$), $8.4 \pm 4.6 \times 10^6$ ($n = 8$), and $7.5 \pm 2.1 \times 10^7$ ($n = 8$), respectively. Detection limits for all concentrations ranged from 1.79×10^4 to 6.91×10^4 fibers/L. For all detectable concentrations, the realized concentrations were within an order of magnitude of the theoretical concentrations. Chrysotile fibers were not detected in New River water ($n = 5$), dechlorinated Blacksburg town water ($n = 14$), and ultrapurified water ($n = 3$) used for laboratory purposes.

96-h Experiments

Corbicula were exposed to suspensions of chrysotile asbestos from May 1983 to August 1984 at 0 (control), 10^2, 10^4, 10^5,

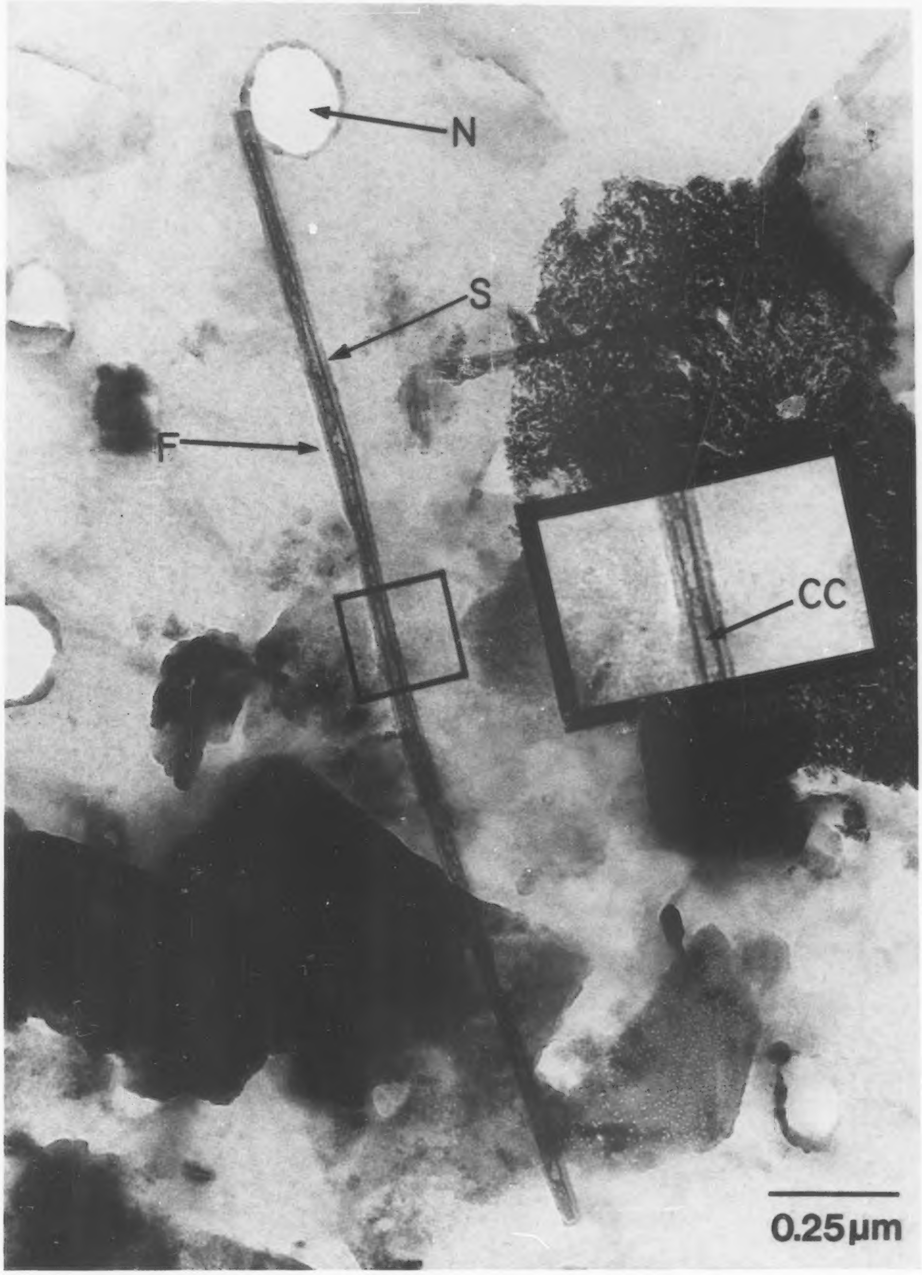

FIG. 1. Chrysotile asbestos fiber (length = 2.141 µm, width = 0.035 µm) isolated from a water sample by the Jaffe-Wick Nuclepore technique. Note the characteristic central canal (CC in insert) and sheath (S) of the asbestos fiber (F). Circular pores (N) from the original polycarbonate filter are 0.2 µm in diameter.

10^6, and 10^8 fibers/L by placing 10 clams on a raised plexiglass platform in a 15-L polycarbonate container (Fig. 2A). The container was held on a stir plate. Stir bars and aeration kept each container well oxygenated and asbestos suspensions uniform. Water chemistry analysis was performed at the initiation and termination of each experiment. The presence of asbestos fibers did not influence water chemistry parameters. The ranges (given as the mean of the concentration giving the lowest and highest values) were as follows: temperature, 19.7–20.5°C; pH, 6.97–7.58; dissolved oxygen, 8.1–8.6 mg/L; hardness, 58.6–66.7 mg/L as $CaCO_3$; alkalinity, 42.2–46.7 mg/L as $CaCO_3$; specific conductance, 116.6–127.8 µS/cm^2; NH_3-N, 0.099–0.215 mg/L; T-PO_4, 4.96–8.03 mg/L; NO_3-N, 5.32–8.49 mg/L; SO_4, 16.88–22.39 mg/L; and

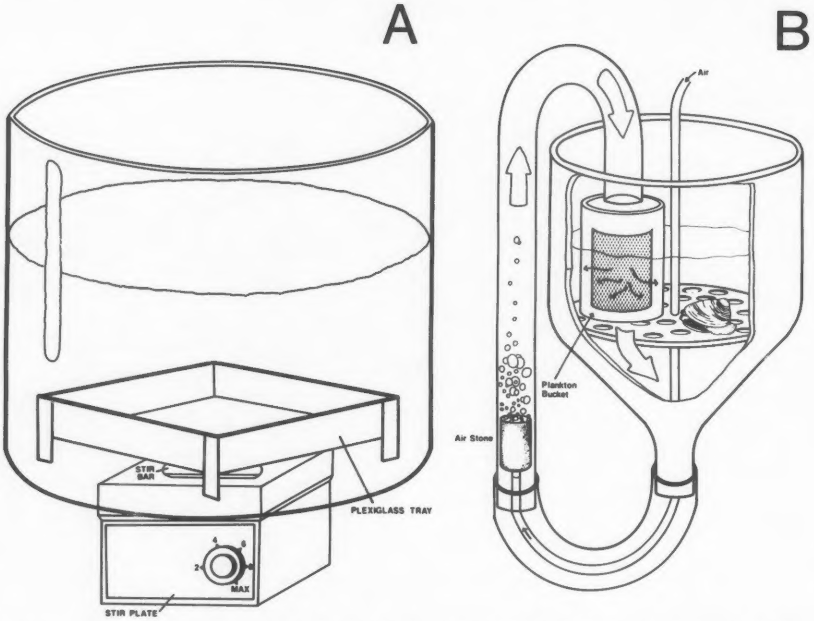

FIG. 2. (A) Exposure system used for asbestos experiments (96 h and 30 d) that employed a raised plexiglass tray above a stir bar used to keep asbestos in suspension. (B) Device used to capture larval *Corbicula* during 14-d exposures to asbestos. The plankton bucket was inserted on sample days to evaluate mortality and number of larvae released by adults.

chloride, 8.25−12.98 mg/L. Anomalously high nutrient levels are a result of feeding the clams on algae cultured in nutrient media (described below). Two sets of experiments were performed: 96 h with ($n = 7$) and without ($n = 5$) food added to the exposure system.

Siphoning behavior was observed at 0, 0.5, 1, 2, 4, 8, 24, 48, 72, and 96 h by counting the number of clams in each container with parted valves. Experiments were performed in an isolated room having a 16 h light : 8 h dark lighting schedule. Clams were housed in a corner at the farthest distance from the door (~8 m) to eliminate disturbances prior to observations. For experiments with food offered, clams were observed 2 h after algae were added to the container (~10:30 a.m. on days 2−4 of each experiment).

The infiltration of asbestos into clam tissue was evaluated at the end of 96-h experiments by the method used by Batterman and Cook (1981), as modified by Patel-Mandlik (1981). Tissue samples were excised and placed in porcelain dishes that were previously sonicated in an acid bath. Each dish was tightly covered with aluminum foil, and the tissue was ashed at 500°C for 8 h. The ash was then suspended in 6 *M* HCl, filtered, and otherwise treated as a water sample in preparation for TEM analysis.

30-d Experiments

Corbicula were exposed to chrysotile for 30 d ($n = 5$) at the same concentrations used in 96-h experiments. Experiments where algae were offered for 96-h exposures were extended to 30 d to evaluate the longer term effects of asbestos on siphoning, growth, gill pathology, and fiber uptake. After the initial 24-h period, clams were observed once daily 2 h after feeding. Growth was determined by measuring each individual at the beginning and end of each experiment for shell growth by Vernier calipers (±0.025 mm precision) and weight (shell plus viscera) by a Mettler PC-440 microanalytical digital balance (±0.0005 g precision). The condition of clams was evaluated at the termination of the experiments by dissecting out visceral and gill tissue, determining wet weight, and drying the sample at 90°C to constant weight (generally 48 h). Percent tissue water was calculated by the following equation:

$$\%\text{TW} = \frac{\text{Wet weight (mg)} - \text{dry weight (mg)}}{\text{Wet weight (mg)}} \times 100.$$

Heath (1984) used this index successfully for bluegill sunfish (*Lepomis macrochirus*) exposed to copper, and elevated water content may represent a generalized response of many organisms to a wide variety of toxicants.

We evaluated the infiltration of asbestos into clam tissue in two ways. First, fiber burdens in gill and viscera were analyzed at the conclusion of each test, using the method described previously. Fiber dimensions in visceral and gill tissue were investigated in two clams exposed to 10^8 fibers/L for 30 d. Length, width, and aspect ratios of fibers were determined from projected micrographs measured by Vernier calipers to evaluate the relationship between water and tissue fiber distributions. Second, the ultrastructure of gill tissue was observed by TEM. Tissue was carefully dissected from clams in a bath of 5% glutaraldehyde buffered with 0.2 *M* phosphate buffer. Tissues were fixed for 24 h in buffered glutaraldehyde, postfixed in phosphate-buffered 0.1% osmium tetraoxide, dehydrated through a graded ethanol series, and flat embedded in Polybed 812 resin. Blocks were cut using an American Optical

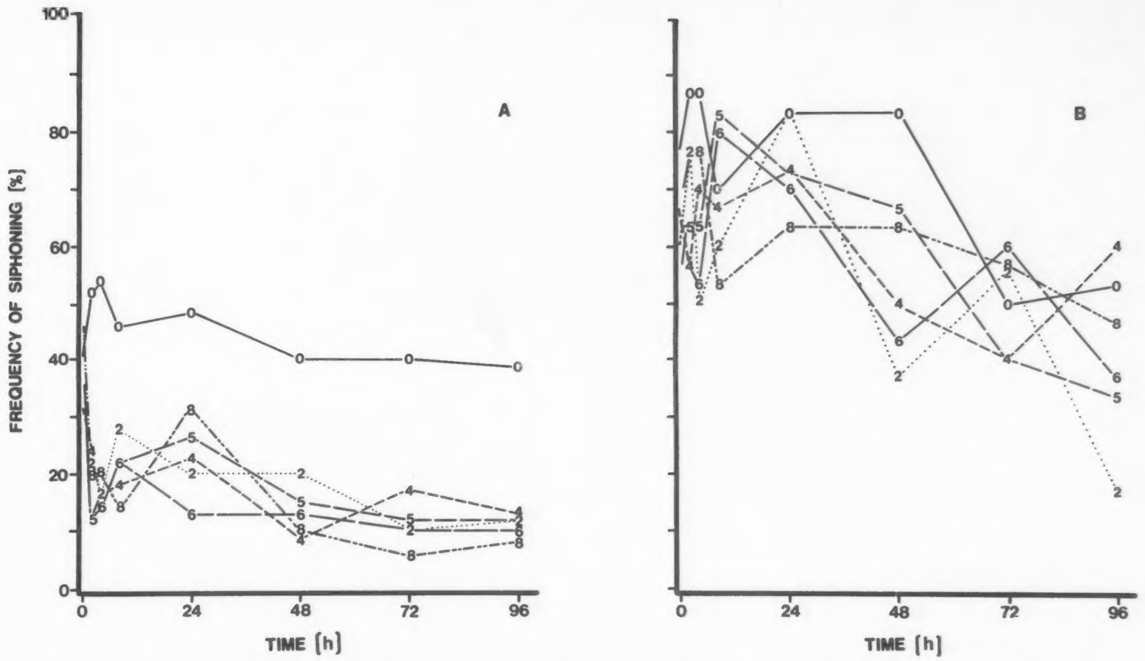

FIG. 3. Mean frequency of siphoning during 96-h experiments (A) with no food and (B) with food; 0, 10^2, 10^4, 10^5, 10^6, and 10^8 fibers/L are denoted by 0, 2, 4, 5, 6, and 8, respectively.

Ultracut microtome with a diamond knife. Thin sections were stained with lead citrate and uranyl acetate and viewed using a JEOL JEM 100C transmission electron microscope. Micrographs of gill tissue were reconstructed in composites to analyze entire gill lamellae by planimetric techniques (Sorenson and Bauer 1984). For water chemistry in 30-d exposures, the ranges (given as the mean of the concentration with lowest and highest values) were as follows: temperature, 19.2−19.5°C; pH, 7.15−7.29; hardness, 67.0−100.0 mg/L as $CaCO_3$; alkalinity, 41.2−56.2 mg/L as $CaCO_3$; specific conductance, 109.8−131.2 $\mu S/cm^2$; NH_3-N, 0.204−0.261 mg/L; T-PO_4, 14.16−21.83 mg/L; NO_3-N, 13.61−17.78 mg/L; SO_4, 18.80−20.59 mg/L; chloride, 12.17−14.93 mg/L.

TABLE 1. Chrysotile asbestos accumulations in adult *Corbicula* exposed in the laboratory (G = gill tissue, V = visceral tissue, W = whole clam homogenate).

Treatment (fibers/L)	Experiment type	Tissue	*n*	Fibers/mg dry weight (mean ± SE)	Detection limit (range)
Control	96 h, no food	G	6	0	15.2−23.2
		V	6	0	16.0−35.1
10^4		G	5	0	17.1−29.5
		V	5	0	18.3−22.0
10^8		G	3	0	29.4−33.4
		V	3	0	20.0−28.7
Control	96 h, with food	W	3	0	16.9−25.8
10^4		W	3	0	21.5−29.8
10^8		W	3	69.1±17.1	29.5−38.2
Control	30 d	G	3	0	18.7−22.3
		V	3	0	14.2−18.6
10^4		G	3	0	19.1−39.2
		V	3	0	30.0−32.0
10^8		G	3	147.3±52.6	18.7−32.4
		V	3	903.7±122.9	29.2−49.4

Larval Release and Mortality

During the spring reproductive season, larval release patterns of *Corbicula* adults (15.5−17.2 mm) were tested during 14-d exposures to asbestos. Clams were held in 2.3-L Buchner funnels designed to accommodate the collection of larvae primarily as veligers (Fig. 2B). A U-shaped tube was fitted to the bottom stem of the funnel and an air stone was inserted. A steady stream of air forced water up a column that was directed back into the funnel; 65-μm-mesh plankton buckets caught larvae circulating in the water column. Replicate containers were used at 0, 10^2, 10^4, 10^6, and 10^8 fibers/L with 10 adults per container. Larval release and mortality were monitored every other day during the 2-wk period of June 11−25, 1984. The plankton bucket was inserted into the chamber for 2 h on the day of collection, allowing sufficient time for 10 complete turnovers of water in the system. A concentrate of veligers and trochophores was subsampled three times from each plankton bucket, and the number of larvae present was counted by using a Sedgewick-Rafter counting chamber (1.0-mL volume). Larval mortality was noted by counting the number of clams with and without mobility. Each larva was observed for movement for at least 1 min. The three subsamples were averaged to determine total larvae released and percent mortality in each container. At the conclusion of the 14-d period, the adults in

TABLE 2. Weight gain and final condition (wet weight, dry weight, and tissue water) for *Corbicula* exposed to chrysotile for 30 d. Sample sizes are indicated below the mean and standard error. Means that are not significantly different, as indicated by the Kruskal-Wallis test, are followed by the same letter ($\alpha = 0.05$).

Parameter evaluated	Asbestos concentration (fibers/L)						Kruskal-Wallis test (p-value)
	0	10^2	10^4	10^5	10^6	10^8	
Weight gain (g)	0.0165±0.0088 (30)	0.0076±0.0075 (30)	0.0063±0.0100 (30)	0.0060±0.0099 (30)	0.0052±0.0112 (30)	−0.0002±0.0103 (30)	0.8979 (>0.95)
Wet weight (g)	0.3043±0.0194 (14)	0.2755±0.0187 (20)	0.2831±0.0214 (18)	0.2998±0.0184 (20)	0.3133±0.0246 (15)	0.3256±0.0156 (13)	2.5535 (>0.75)
Dry weight (g)	0.0423±0.0038 (14)	0.0349±0.0032 (20)	0.0376±0.0038 (18)	0.0356±0.0029 (20)	0.0383±0.0045 (15)	0.405±0.0035 (13)	4.2528 (>0.50)
Tissue water (%)	86.10±0.34 a (14)	87.33±0.42 b (20)	86.74±0.91 ab (18)	88.29±0.36 b (20)	87.81±0.63 b (15)	87.56±0.39 b (13)	12.4164 (<0.05)

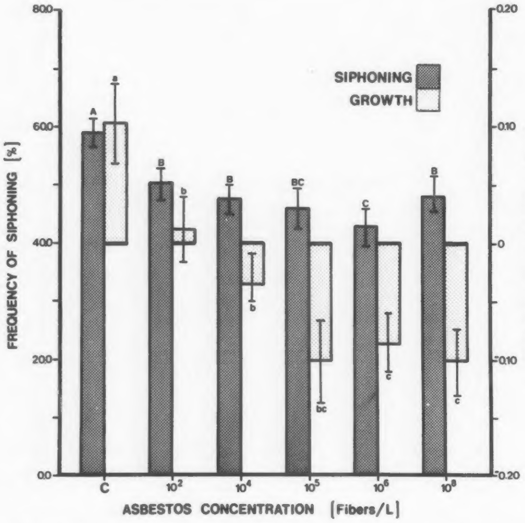

FIG. 4. Siphoning activity and growth of *Corbicula* during 30-d exposure to chrysotile. For siphoning data, the Kruskal-Wallis test indicated significant differences between groups ($n = 100$ for all treatments, $\chi^2 = 21.589$ with 5 df, $p < 0.005$). Means with the same capital letter are not significantly different ($\alpha = 0.05$). For shell growth data the Kruskal-Wallis test also indicated significant differences between groups ($n = 30$ for all greatments, $\chi^2 = 23.843$ with 5 df, $p < 0.005$). Means with the same lowercase letter are not significantly different ($\alpha = 0.05$).

each chamber were sacrificed and the tissue was excised and dried. Numbers of larvae collected on each day were scaled to numbers released per milligram of total adult tissue dry weight in each container to account for differences in size among the adults.

Statistical Analysis of Data

Nonparametric statistical techniques were applied in all analyses to ensure uniformity of interpretation because not all data were normally distributed. A one-way analysis of variance rank analogue, the Kruskal-Wallis test, was applied for one-way layout data (Hollander and Wolfe 1973). This included observations of siphoning behavior at each observation time for all experiments, clam growth and condition data for 30-d exposures, fiber dimension analysis for 30-d exposures, and larval clam mortality and release patterns for 14-d tests. If significant differences were indicated by the Kruskal-Wallis test ($\alpha = 0.05$), a rank-like least significant differences (LSD) procedure was used to determine which means were significantly different. In all comparisons of means, standard errors were calculated. In cases of two-sample data (i.e. planimetric analysis of gill tissue), Wilcoxon's rank sum was used to test differences between means (Hollander and Wolfe 1973).

Results

96-h Exposures Without Food

Corbicula reduced siphoning activity upon exposure to chrysotile (Fig. 3A). Siphoning activity was depressed quickly (in 8 h), and all asbestos exposures had nearly equal effect in reducing siphoning activity. By 48 h, all asbestos-exposed groups siphoned significantly less than controls ($\chi^2 = 12.215$, $p < 0.05$); by 72 h, all asbestos-exposed *Corbicula* siphoned with similar frequency at one-third the level of control activity ($\chi^2 = 17.375$, $p < 0.05$).

Chrysotile fibers were not observed in either gill or viscera of any *Corbicula* exposed for 96 h without food (Table 1). Detection limits were calculated by assuming that one fiber was present in the sample (Anderson and Long 1980). Generally less than 30 fibers/mg were found.

96-h Exposures With Food

When *Corbicula* were offered *Chlamydomonas*, they siphoned more often in all exposures relative to nonfeeding experiments (Fig. 3B). Siphoning frequency was not suppressed as observed in asbestos-treated clams, and no significant differences were found in these experiments ($\chi^2 = 2.328$, $p > 0.05$ at 96 h). Lower siphoning activity in all treatments by 72−96 h was probably due to satiation, as substantial amounts of pseudofeces were observed in the plexiglass trays.

Chrysotile fibers were not observed in control and clams exposed to 10^4 fibers/L at the conclusion of the 96-h observation period. At 10^8 fibers/L an average of 69.1 fibers/mg was found which was approximately two times above the detection limit (Table 1).

30-d Exposures

Siphoning activity was depressed upon exposure to asbestos in five 30-day experiments (Fig. 4). Control and asbestos-exposed clams siphoned ~60 and ~40−50% of the time, re-

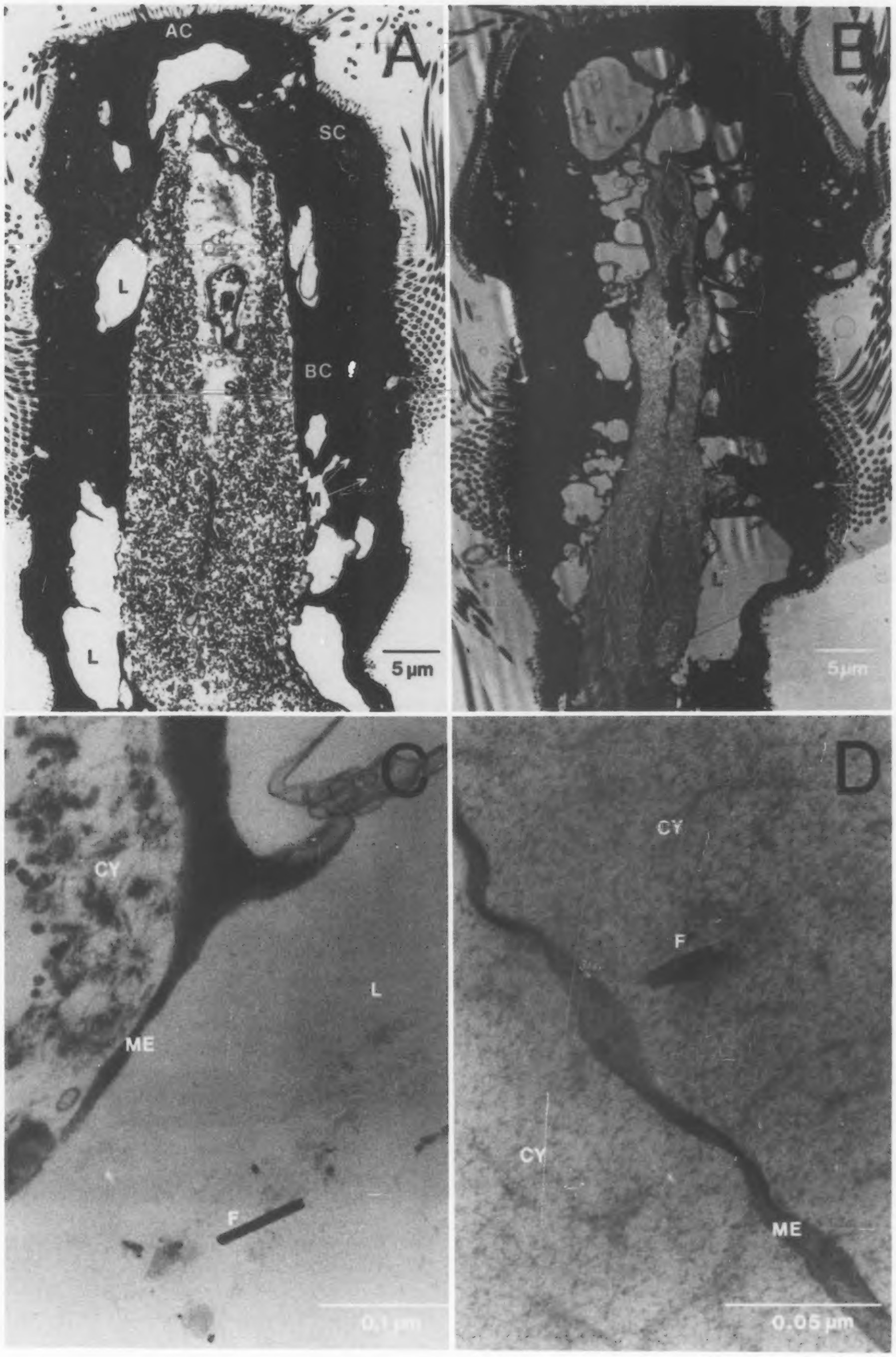

FIG. 5. (A). Gill lamella from a control clam held in the laboratory for 30 d. Locules (L) are interspersed among basal (BC) and apical (AC) ciliated cells and secretory cells (SC). Ciliated cells are mitochondria (M) rich. A central support cell (S) lies inside the peripheral cells and locules. (B) Gill lamella from a clam exposed to 10^8 fibers/L chrysotile for 30 d. Locules appear with significantly greater frequency and occupied greater surface area than controls. (C) Chrysotile fibers (F) were found most often in gill locules. No fibers were observed in direct association with cell membranes (ME). (D) Two fibers were found in the cytoplasm (CY) of ctenidial cells.

spectively. Control siphoning was significantly greater than all asbestos-exposed groups, which among themselves were essentially equal.

During these same 30-d experiments, *Corbicula* grew most in control chambers with an average increase in shell length of 0.105 ± 0.034 mm (Fig. 4). Controls were significantly greater than asbestos-exposed groups of 10^4, 10^5, 10^6, and 10^8 fibers/L, some of which decreased in shell length. A similar, but statistically not significant trend was apparent in weight gain and final dry weight (Table 2). Weight gain was confounded by a change in percent tissue water which was significantly lower in control than asbestos-treated clams. The increases in tissue water, although slight (1−2%), may account for no observable differences in final wet weights of *Corbicula* receiving asbestos exposure.

After a 30-d exposure to 10^8 fibers/L, clams accumulated ~150 fibers/mg in gill and 900 fibers/mg in visceral tissues (Table 1). However, no accumulation was apparent at 10^4 fibers/L, a concentration which was below detection in water.

Measurements of fiber dimensions from two clams exposed to 10^8 fibers/L revealed that smaller fibers were present in gill and visceral tissues than water. Fibers suspended in water (W) averaged 6.53 ± 2.34 μm long and 0.67 ± 0.11 μm wide ($n = 100$); in gill tissue (G), fibers were 1.21 ± 0.96 μm long and 0.05 ± 0.03 μm wide; in visceral tissue (V), fibers were 3.94 ± 2.10 μm long and 0.48 ± 0.32 μm wide. The Kruskal-Wallis test indicated that for length, $G < V < W$ ($\chi^2 = 21.41$, $p < 0.005$) and for width, $G < V = W$ ($\chi^2 = 17.29$, $p < 0.005$). The mean aspect ratio (length/width) was 9.7 for W, 24.2 for G, and 8.3 for V.

Gill tissue from controls and clams exposed to 10^8 fibers/L was analyzed by TEM. In gill tissue of controls, the central support cell is surrounded by unciliated secretory cells and ciliated cells located apically and basally on the lamella (Fig. 5). Open locules, which are apparently fluid filled, are evenly dispersed along the support cell (Fig. 5A). Locules were 14.01 ± 1.96% of the total surface area of the lamella as measured ($n = 5$). An average of 21.4 ± 4.8 locules were observed in each gill lamella. Gill tissue from clams exposed to chrysotile for 30 d possessed significantly more locules in each lamella, 25.7 ± 3.2 (Wilcoxon rank sum = 48.0, $p < 0.005$), and locules occupied significantly greater surface area of the lamellae, 26.72 ± 2.17 (Wilcoxon rank sum = 51.0, $p < 0.001$) (Fig. 5B). Eleven asbestos fibers were observed embedded in gill tissue. Eight fibers (72%) were in locules, apparently not embedded in a tissue matrix (Fig. 5C). Two fibers were located in connective ctenidial tissue (Fig. 5D), and one fiber was deposited in an apical ciliated cell. At no time were chrysotile fibers found in association with cellular isolating mechanisms (e.g. vacuoles, collagen, or macrophages).

Larval Release Patterns

Control gravid clams released larvae at the rate of 175−800 veligers/adult every 2 d. Larvae released by adults exposed to asbestos fell as low as 10/adult every 2 d in 10^8 fibers/L. On an adult dry weight basis, the numbers released in control, 10^2, 10^4, 10^6, and 10^8 fibers/L were 29.23 ± 10.15, 14.43 ± 6.21, 9.03 ± 4.19, 5.97 ± 5.28, and 7.58 ± 2.65, respectively. The Kruskal-Wallis test indicated release in the order control > $10^2 > 10^4 > 10^6 = 10^8$ fibers/L ($\chi^2 = 29.735$, $p < 0.005$). During this same period, the percent mortality of veligers from control, 10^2, 10^4, 10^6, and 10^8 fibers/L treated groups was 11.26 ± 2.19, 18.26 ± 7.15, 25.13 ± 6.14, 26.69 ± 9.77, and 27.60 ± 8.73, respectively. The Kruskal-Wallis test indicated mortality in the order control $< 10^2 = 10^4 = 10^6 < 10^8$ ($\chi^2 = 23.914$, $p < 0.005$).

Discussion

We have shown that asbestos exposure reduces the siphoning activity of *Corbicula*. Reductions in siphoning were 10−20% of control activity at all exposures over a 30-d period. All levels of asbestos caused significant reductions in shell growth, and the same trend existed for weight gain over the 30-d period. These observations are consistent with studies by Foe and Knight (1985) who fed *Corbicula* a diet of algae and small particulate inorganic sediment (98% was smaller than 64 μm, and the modal size was 14 μm) in varying concentrations. Growth was significantly lower in groups fed particulates and algae than algae alone, perhaps due to the inability of clams to distinguish between organic and inorganic matter. In our study, when no food was offered in 96-h experiments, exposed clams rapidly reduced siphoning activity to one-third the level of controls. However, when food was offered, this inhibitory effect was overriden and siphoning frequency remained unaltered. Controls exhibited shell and tissue growth, and our findings are similar to those of Dauble et al. (1985) and Foe and Knight (1986) who investigated nutritional needs of *Corbicula*. Dauble et al. (1985) determined that ~1000 cells/mL (summer phytoplankton density) gave adequate growth, while 350 cells/mL (winter phytoplankton density) did not. Foe and Knight (1986) found that a diet of three green algae (*Chlamydomonas*, *Chlorella*, and *Ankistrodesmus*) gave superior growth compared with di-algal formulations at 1×10^6 cells/mL in 10-L aquaria with 18 clams/aquarium. In our study (10 clams/15 L), the effective algal concentration per clam was 1.5×10^6 cells per day, whereas Foe and Knight (1986) used 5.5×10^8 cells per day. In comparison, both these values are at or above the upper limit of river phytoplankton densities (Hynes 1970; Cohen et al. 1984), and it is apparent that the nutritional and ecological needs of *Corbicula* need to be investigated further in the laboratory relative to growth potential in freshwater rivers.

We have shown that *Corbicula* is an efficient accumulator of chrysotile asbestos. Uptake is relatively low in short-term 96-h experiments but is well above the level of detection at 10^8 fibers/L of exposure and is consistent with 30-d fiber burden observations. The body burdens reported in this study upon exposure to 10^8 fibers/L for 30 d represent the greatest body concentration known for this duration of exposure. In 30-d tests, the uptake of fibers also inhibited growth and suppressed siphoning activity. Kidneys from arctic char that experienced 3−4 yr of exposure to 10^8 fibers/L had 230 fibers/mg (Batterman and Cook 1981). Patel-Mandlik (1981) reported that human subjects with lifetime exposures to asbestos developed kidney tumors and had levels of 9500 fibers/mg in kidney tissue. Halsband (1974) reported that mussels exposed to chrysotile accumulated fibers and blocks of asbestos which remained embedded after mussels were transferred to clean water. From these observations and our study, it appears likely that clams may bioaccumulate fibers through a lifetime of exposure. Fibers suspended in water do not represent the only source of chrysotile to clams. Lauth and Schurr (1983, 1984) exposed a phytoflagellate (*Cryptomonas erosa*) to chrysotile. Algal cells deposited fibers internally and fibers also adhered externally to them; therefore, food sources may represent another vector for fiber uptake in suspension-feeding bivalves.

We have presented evidence for pathological and toxicological effects of chrysotile to *Corbicula*, in addition to inhibition of growth and siphoning. Tissue water content of clams exposed to chrysotile for 30 d increased relative to controls. This is consistent with our electron microscopy observations of gill tissue where fluid-filled spaces were significantly increased in number and size upon exposure to 10^8 fibers/L. Fibers also were isolated in locules more frequently than in other gill regions. The size distribution of asbestos fibers in water versus that in the tissues of clams indicates that small fibers were taken up more easily. Small, thin particles are biologically more interactive than large, blocky particles (Cook et al. 1982; Hesterberg and Barrett 1984). Intracellular distributions, phagocytosis, transport, and clearance of fibers are believed to be correlated with fiber size, with small, high aspect ratio fibers being most mobile (Selikoff and Lee 1978; Cook 1983). Fibers in visceral tissue were intermediate in size between water and gills, probably due to the presence of some larger fibers that were not yet embedded in the visceral area but may have been moving through the gastrointestinal tract of the clam.

Mortality of adults was not observed in 96-h experiments and was not significant in 30-d tests. Belanger et al. (1985) demonstrated that mortality for fish was not enhanced by asbestos exposure in 2- to 3-mo tests at 10^6 fibers/L, but that pathologic and behavioral effects were evident and were better indicators of subtle, potentially chronic effects. In our study, asbestos exposure increased larval mortality by 7 to 17% in 10^2-10^8 fibers/L relative to controls. The effect on recruitment to *Corbicula* populations is difficult to infer, since no published studies exist on natural survivorship of veliger *Corbicula*. Stewart and Schurr (1980) demonstrated that larval *Artemia salina* had 20% mortality above baseline control mortality after 24-h exposures to 10^7 chrysotile asbestos fibers/L.

To date, chrysotile asbestos has not been regarded as a significant water quality problem for aquatic life. Amphibole asbestos is a well-documented contaminant of Lake Superior but is disregarded in environmental contaminants programs of the Great Lakes (Shear 1981). This neglect is probably due to the fact that the majority of toxicity information generated for bivalves and fish has been from acute exposure type with mortality as the end point. Effects of asbestos on *Corbicula* at levels known to occur in the environment that we present here include growth inhibition, alteration of siphoning behavior, gill tissue degradation, and reduced condition with a concomitant uptake of chrysotile fibers. This study imparts two final caveats. First, clams may become useful indicators of asbestos contamination, since they are efficient accumulators of fibers. Lifetime exposures, even at nondetectable fiber concentrations (e.g. $<10^5$ fibers/L) in water, may result in detectable tissue concentrations. This result is not surprising, for the potential value of bivalves as accumulators and indicators has been demonstrated for organic compounds (Hartley and Johnston 1983) and heavy metals (Graney et al. 1983). Second, and more important, this and recent studies by Woodhead et al. (1983), Lauth and Schurr (1983, 1984), and Belanger et al. (1985) dictate that a review of the effects of asbestos on aquatic life is needed. The previously "low confidence" in the bioaccumulation data base for asbestos by aquatic organisms (U.S. Environmental Protection Agency 1979) has now changed and we are moderately confident that bioaccumulation is possible at all trophic levels. Recent programs instituted by the U.S. Environmental Protection Agency in California include establishing a coastal monitoring program for asbestos in mussels (Brian Melzian, USEPA, Region IX, 215 Freemont St., San Francisco, CA 94105, pers. communication). Caution is warranted, as industrial use and environmental distribution of chrysotile continues to expand and the potential impact by asbestos is increased on humans, fish, and shellfish.

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High-Density Culture of Meiobenthic Harpacticoid Copepods Within a Muddy Sediment Substrate

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Chandler, G. T. 1986. High-density culture of meiobenthic harpacticoid copepods within a muddy sediment substrate. Can. J. Fish. Aquat. Sci. 43: 53–59.

Difficulties in producing a muddy substrate which does not easily foul have made previous efforts to culture mud-inhabiting, estuarine, and marine harpacticoid copepods unsuccessful. Natural, organic-rich muds are unsuitable as a long-term culture medium because they generate detrimental bacterial blooms in stagnant and periodically flushed culture systems. I present some simple procedures to (1) sort muddy sediments into a <125-μm size class, (2) flush away most dissolved organics, (3) sterilize the sediments providing a moderately foul-free culture medium, (4) generate a life-like, flocculent surface layer, and (5) allow easy observation above or below the sediment surface. Five harpacticoids were cultured within 45–90 d to densities 4–11 times their natural field maxima (per 10 cm^2): *Scottolana canadensis* (372), *Paronychocamptus huntsmani* (380), *Onychocamptus mohammed* (448), *Cletocamptus deitersi* (1259), and *Nitocra lacustris* (1662). Since most mud-inhabiting harpacticoids are larger than 125 μm, simple sieving on a 125-μm screen eliminates culture sediments leaving behing hundreds of clean, easily collected harpacticoids.

Le fait qu'il soit difficile de produire un substrat vaseux qui ne devient pas fétide facilement a fait échouer les efforts antérieurs visant à élever des copépodes estuariens et marins du groupe des harpacticoïdes qui vivent dans la vase. Les vases naturelles, riches en matières organiques, sont peu appropriées comme milieu de culture à long terme, car elles sont le siège de proliférations de bactéries nuisibles dans les milieux d'élevage stagnants et nettoyés périodiquement. Je présente quelques techniques simples pour (1) classer les sédiments vaseux dans une catégorie de taille <125 μm, (2) éliminer la plupart des substances organiques dissoutes, (3) stériliser les sédiments en fournissant un milieu de culture passablement exempt de matières fétides, (4) produire une couche superficielle floculeuse qui semble vraie et (5) permettre une observation aisée au-dessus et en-dessous de la surface des sédiments. On a élevé cinq harpacticoïdes pendant 45 à 90 j à des densités de 4 à 11 fois supérieures au maximum rencontré dans leur habitat naturel (par 10 cm^2), soit les espèces *Scottolana canadensis* (372), *Paronychocamptus huntsmani* (380), *Onychocamptus mohammed* (448), *Cletocamptus deitersi* (1259) et *Nitocra lacustris* (1662). Comme la plupart des harpacticoïdes qui vivent dans la vase sont plus gros que 125 μm, un simple tamisage à l'aide d'une grille de 125 μm élimine les sédiments du milieu de culture en laissant des centaines d'harpacticoïdes propres qu'on peut recueillir facilement.

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One of the primary obstacles to the development of a productive and economical mariculture for commercial fishes has been providing an acceptable food source, especially for the juvenile stages. Many juvenile marine and estuarine fishes pass through a critical stage where they are dependent on benthic prey, especially harpacticoid copepods. For example, some juvenile salmonids (Sibert 1979), pomadasyids (Alheit and Scheibel 1982), and pleuronectids (Tito de Morais and Bodiou 1984) pass through an obligate harpacticoid feeding period lasting from 2 wk to 8 mo before other food resources are utilized. Harpacticoid copepods are probably a better nutritional source than many other meiofauna-sized (<1 mm) prey (Hicks and Coull 1983), and can promote faster growth rates than other copepods or amphipods (Volk et al. 1984).

Unfortunately, methods for culturing large numbers of harpacticoids as food for fish are available for only a few large epipsammic and semiplanktonic species (e.g. *Tisbe* spp. and *Tigriopus* spp. (Kinne 1977) and *Schizopera elatensis* (Kahan et al. 1981)). These species have been used to a limited extent in fish mariculture with only mixed success (Fijita 1977). Success might be improved if high densities of a wider variety of species more typical of the kinds found in stomachs (e.g. small, infaunal sand- or mud-dwelling forms) could be cultured and fed to the small-mouthed juvenile stages.

Additionally, studies of meiobenthic populations and communities have been limited to largely mensurative (sensu Hurlbert 1984) and more recently manipulative field studies (for reviews, see Hicks and Coull 1983; Coull and Palmer 1984). Culture methods necessary to provide large numbers of specimens for controlled laboratory experimentation have been inadequate or unavailable for most species. As a result, what little is known about harpacticoid behavior, life histories, intra- and interspecific competition, population dynamics, and interactions with micro- and macrofauna has usually been inferred from field surveys and short-term field experiments. Published accounts of direct observations of these phenomena either in the field or in the laboratory are few (Palmer 1984; Chandler

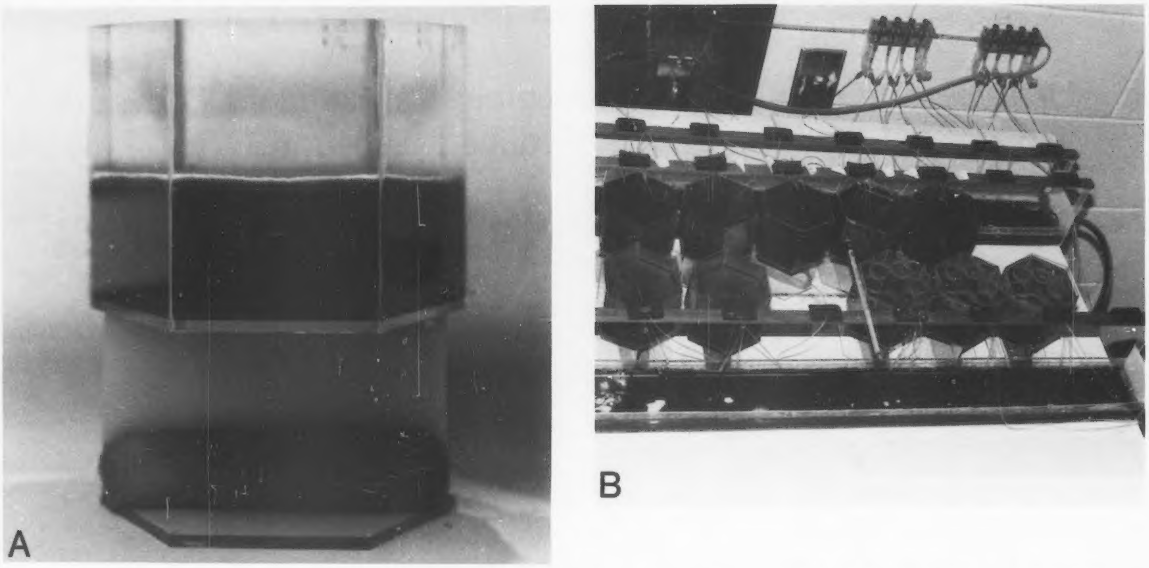

FIG. 1. (A) Close-up of a culture vessel showing the general hexagonal design (with vertical support and clay hinge) and the flocculent sediment surface; (B) drip-through culture system showing culture vessels, tubing, and overflow troughs.

and Fleeger 1984; Marcotte 1984). This is unfortunate, as strong substantiation of inferences from field data is best supported by direct observational evidence.

Very few truly sediment-dwelling harpacticoid species have been cultured successfully, and rarely at densities very much above inoculation (i.e. maintenance) levels. Their strong dependence on a sand or mud substrate of a particular size, texture, microfaunal/microfloral composition, etc., for food, reproduction, and protection has precluded easy cultivation in the laboratory. My purpose was to find simple, efficient, and economical ways to (1) cleanse and sterilize muddy sediments for use in normal or high-density culture of mud-inhabiting harpacticoids, (2) reconstruct a foul-free, reasonably life-like imitation of the natural sediment structure to promote natural copepod behaviors and life histories, and (3) photograph surface/subsurface behaviors and biogenic effects on a controlled, predetermined sediment structure. Harpacticoids cultured by such techniques would then be available for trophic or maricultural studies, as well as controlled laboratory studies of muddy-bottom meiofaunal activities.

Materials and Methods

Preparation of Culture Medium

Copepods were cultured in a muddy sediment medium prepared as follows. Two 19-L buckets of fresh, predominately silt−clay surface (0−3 cm) sediments were collected by hand from a mudflat in a *Spartina alterniflora* marsh near Cocodrie, Louisiana, and refrigerated or frozen until ready for use.

Sediments were washed with deionized water through a 0.5- and 0.125-mm sieve set (30-cm diameter) stacked flush over a cylindrical Pyrex® jar (30.5 × 305 cm; 17 L). Most of the silt and fine-sand fraction passing through the 0.125-mm sieve was captured in the jar, but the lighter clay and detrital particles and unwanted organics (humic acids, tannins, etc.) were flushed away by allowing the washwater to slowly overflow the jar.

After sieving and washing, the sediments in the jar were allowed to settle for 1 h until a distinct precipitation band formed between the uppermost layer of remaining clay-size particles and the heavier silt and fine-sand fraction. The lighter clay-size fraction was aspirated away to the precipitant band and discarded. The jar was refilled with deionized water, stirred vigorously, allowed to settle for 90 min, and again aspirated to the precipitant band.

The remaining heavy fraction was condensed to 50% original volume by heating in a drying oven for 24 h at 120−140°C. The medium was stirred every 6−8 h and removed when the 50% reduction was achieved. Perforated aluminum foil was placed over the bell jar to control the evaporation rate, thus reducing surface dehydration and clumping. The condensed medium usually contained shrinkage cavities filled with unwanted organic leachate. After cooling, the leachate was aspirated away.

The cooled medium was vigorously blended using an electric cake mixer until a consistency like pudding was achieved. This ensured that all sediment particles were dispersed uniformly. Portions (600 mL) of blended sediment were then ladled into 1-L beakers, covered with heavy duty foil, autoclaved (107°C, 4.5 $\mathrm{kg \cdot cm^{-2}}$, 40 min), and stored indefinitely under refrigeration. Yield of culture medium was 50−60% by weight of original natural sediments with a median grain diameter (MGD) of 0.02 mm and total organic matter (TOM) content of 7% (natural sediments = 0.04-mm MGD; 10% TOM).

Autoclaving semisolidified the medium, but it was rehydrated to natural texture by blending with artificial seawater (ASW) 1 to 1 or less to make "wet" medium. The proportion of medium to ASW that yielded the most natural reconstitution had to be determined experimentally, as the final texture of the autoclaved medium depended upon the original composition of the natural source sediment.

Artificial generation of a flocculent surface layer was necessary to achieve a realistic imitation of the natural sediment structure. Most mud-inhabiting harpacticoids live almost ex-

TABLE 1. Maximum mean densities per 10 cm^2 ± SE of five mud-inhabiting harpacticoid copepods after 40–60 d of culture based on fourteen 0.63-cm^2 core samples per culture of *Nitocra lacustris*, *Cletocamptus deitersi*, and *Scottolana canadensis*. Densities of *Paronychocamptus huntsmani* and *Onychocamptus mohammed* are based on total counts.

Species	Females	Males	Copepodites	Total
Nitocra lacustris	1274 ± 173	42 ± 9.5	346 ± 33.4	1662 ± 161
Cletocamptus deitersi	328 ± 14.0	480 ± 43.0	451 ± 28.8	1259 ± 88
Scottolana canadensis	236 ± 31.4	36 ± 9.2	100 ± 13.3	372 ± 40.9
Paronychocamptus huntsmani	—	—	—	380
Onychocamptus mohammed	—	—	—	448

clusively in the flocculent top 1 cm of muddy sediments (Coull and Bell 1979; Chandler and Fleeger 1983), grazing on it, reproducing in it, and even filtering the floc (e.g. *Scottolana canadensis* (Harris 1977)). Therefore, a 3-cm base layer of wet medium was poured into the culture vessels and covered by a 1-cm-thick flocculent layer prepared as follows. Dry medium (20 g) was placed into a 150-mL beaker, brought up to 130 mL with 5% $Na(PO_3)_6$ in ASW, and stirred vigorously. It was then sonicated for 15–20 min and placed in a refrigerator to soak for 4 h. The $Na(PO_3)_6$ neutralizes electrostatic bonding of clay particles and aids dispersion (see Buchanan 1971). After soaking, the sediments settled out of suspension and the remaining supernatant was aspirated away and replaced with aerated ASW. The mixture was stirred and sonicated for 10 min to complete the preparation.

Preparation of Culture Vessels for Surface/Subsurface Observation

Copepod culture and experimentation was carried out in hexagonal observation vessels (75 mm high × 100 mm wide; surface area = 66 cm^2) made from glass and Plexiglas (Fig. 1A). A 3.0-cm-deep layer of wet medium was poured into each vessel (sed. vol. = 200 cm^3) and leveled by gently tapping the vessel on a laboratory bench. Each vessel was held upright 55 mm above a hexagonal base by a rectangular Plexiglas strip inserted vertically into a modeling-clay hinge. The hinge provided support and allowed the upright angle of the vessel to be easily adjusted for oblique viewing. Because the six sides were glass, faunal activities above and below the sediment–water interface could be observed and photographed through any wall (or from above) with a stereophotomicroscope placed orthogonal to the glass walls. To prevent algal growth and discourage edge artifacts, the portion of each glass wall adjacent to the sediment can be covered with a removable 3.0-cm strip of aluminum foil lined with cellophane to protect the glass.

The flocculent surface was added to the wet medium base as follows. Fresh aerated ASW (100 mL) was added slowly to the medium surface with a small-bore squeeze bottle. Any medium adhering to the ASW surface film was aspirated away. The 130 mL of prepared floc was then stirred vigorously and immediately poured (slowly) into the culture vessel. The final water level was 1 cm below the vessel lip. The flocculent sediments were allowed to settle for 2 h before connecting the vessel to a "drip-through" flow system. ASW was delivered very slowly to each vessel through small-bore (20 gauge) polyethylene catheters (Fig. 1B). Flow through the catheters was gravity fed and controlled by standard aquarium gang valves (Lustar® brand). Two catheters were connected to each gang via a Y-tube. The preparation was flushed for 24 h at a drip rate of 1.0–2.0 mL·min^{-1} before fauna were added. A fluorescent light regime of 12 h light : 12 h dark promoted a healthy growth of incidental benthic diatoms in the cultures.

Successful cultures were started with as few as 30 gravid copepods, but they reached maximum density more quickly if 100 or more gravids were introduced initially. Inoculating copepods were pipetted from natural sediments as soon after collection as possible, washed gently several times with ASW to remove most adhering ciliates and debris, and then slowly pipetted into culture vessels. The drip-through system was turned off for 1 h to allow the animals to settle into the culture medium. If a species had planktonic nauplii, the capillary tubes in the usual position would draw the nauplii into the overflow trough. This was prevented by placing the capillary mouth on the top edge of a glass wall so that a thin ASW film crept into it as the water level rose. If the nauplii were photopositive (e.g. *Scottolana canadensis*), a small fluorescent lamp placed opposite the capillary outflow side also helped to prevent loss.

Capillary action generated a dripping outflow for each vessel. Two glass capillaries made from the capillary ends of 22.5-cm Pasteur pipettes were bent 45° at 6 cm and 20° at 2 cm so as to contact the ASW surface film. Each catheter and capillary set was clamped 5 mm above the ASW surface by uniformly spaced velcro pads (2 × 2 cm) mounted on a flat horizontal wooden bar (85 × 2 cm) supported 13.5 cm above a Plexiglas overflow trough (85 × 8 × 45 cm). Capillaries were removed monthly and acid cleaned (6 mol HCl/L) to prevent clogging and loss of capillary action. Continuous dripping at 0.5–1.0 mL·min^{-1} maintained foul-free cultures for up to 12 mo. If the drip rate was slower than 0.5 mL·min^{-1}, the organic-rich culture medium would occasionally foul.

Feeding and Harvesting

Harpacticoids were fed a mixed diet of chrysophytic (*Isochrysis galbana*) and chlorophytic (*Dunaliella tertiolecta*) algae, one diatom species (*Thallassiosira weissflogii*), and spinach fragments. The spinach fragments were prepared by blending 10 g of frozen spinach at high speed in 500 mL of ASW for 3 min, washing it through a 45-μm screen, and collecting the sieved fraction in a 1-L beaker. Any foamy residues remaining on the surface of the spinach solution were aspirated away. Young cultures of 200 copepods or less were fed 10 mL of an equal, four-part suspension of each of the three algal types and the spinach solution every 3 d. Mature cultures were given 30 mL every 2 d. If food accumulated on the sediment surface, cultures were not fed until it disappeared; otherwise, fouling would occur. Algae were cultured on F/2 medium (Guillard 1972) in 500-mL Erlenmeyer flasks.

High-density cultures were nondestructively harvested as follows. A 3-mm-bore Pasteur pipette was connected to a 500-mL side-arm vacuum flask with 1 m of gum-rubber tubing

TABLE 2. Previous methods used to culture or maintain harpacticoid copepods in the laboratory. natural seawater; ASW = artificial seawater. See Kinne (1977) review for *Tisbe* spp. and *Tigri*

Species (habitat)	Culture medium	Culture apparatus	
Paronychocamptus nanus (sand) *Tachidius discipes* (sand/muddy sand)	70 mL asbestos-filtered NSW with 50% replaced bidaily	Glass tubes (10 × 3.5 cm) kept at 10°C in water bath	*Tetrasel* *Phae* *tricor* each) lyoph every
Microlaophonte sp. (muddy sand)	Corn meal agar mixed 1/2 strength with NSW, scored, and covered with NSW film	Sealed Petri dishes (9.3 × 1.7 cm) kept on 12:12 LD for 3 mo	Incident
Thompsonula hyanae (sand)	Dried autoclaved sand from natural habitat and filtered NSW	Covered finger bowls (8-cm dia) kept on 12:12 LD in summer, 10:14 LD in winter	Mixture diato incid
Nitrocra typica (salt-marsh aufwuchs)	Solidified erdschreiber covered with Millipore-filtered (0.45 μm) NSW containing antibiotics and antimycotics (pencillin, 10 000 U·mL^{-1}; streptomycin, 10 g·mL^{-1}; fungizone, 25 μg·mL^{-1}); stocks transferred every 3 wk	Petri dishes (10 × 1.5 cm) kept at 25°C on 18:6 LD	*Cylindr* (1 ×
Scottolana canadensis (mud/sandy mud)	100 mL Millipore-filtered (0.45 μm) NSW (10‰)	125-mL Erlenmeyer flasks kept in darkness	Mixture *galba* *pseud*
Paramphiascella vararensis (sand)	Unsorted, acid-cleaned, autoclaved beach sand overlain by 80 mL coarse-filtered and autoclaved NSW	Covered evaporating dishes (100 mL) illuminated fluorescently on 12:12 LD at 18°C	Mixture crab, yeast. urchi *Aster* fish f slight
Asellopsis intermedia (sand)	NSW and metazoan-free beach sand (3-grain thickness), agitated by aeration, and renewed every 5 d	Polyethylene specimen tubes with bases and lids replaced by 75-μm mesh; suspended in flow-through aquaria	"Probab on sa
Tachidius discipes (sand/muddy sand)	200 mL filtered NSW (26‰)	— (reared in darkness with NSW changed daily)	*Tetrasel*

oratory. Densities are given where provided by the author(s). NSW = natural seawater; ASW =
d *Tigriopus* spp. culture.

Food	Inoculation density	Maximum density	Reference
Tetraselmis suecica and *Phaeodactylum tricornutum* (0.2 mL each) and a few drops of lyophilized detritus; fed every 3–4 d	1 gravid·tube^{-1}	— (60–87% survival of *P. nanus*; 75–81% for *T. discipes*)	Smol and Heip 1974
Incident microflora/fauna	"A few gravids"	— (100% survival of 20 adults and 20 larvae for 2 wk)	George 1975
Mixture of 2 naviculoid diatom spp. and incidental bacteria	—	No net growth; all dead in 12–13 d	Sellner 1976
Cylindrotheca closterium (1 × 10^4 cells·dish^{-1})	2 gravids·dish^{-1}	159·dish^{-1} (all stages)	Lee et al. 1976
Mixture of *Isochrysis galbana* and *Thallassiosira pseudonana* (10 mL·wk^{-1})	— (batch inoculation of nauplii)	—	Harris 1977
Mixture of ground herring, crab, mussel meat, baker's yeast, cottage cheese, urchin gonads, *Ulva*, *Asterias*, and Tetra Min fish food; all given in slight excess	—	—	Rieper 1978
"Probably bacterial epigrowth on sand-grains"	—	30·tube^{-1} maintained up to 9 mo	Hardy 1978
Tetraselmis suecida	50 detached egg sacs; unhatched sacs removed after 2 d	—	Teare and Price 1979

TABLE 2. (*Concluded*)

Species (habitat)	Culture medium	Culture apparatus	Fo
Amphiascella subdebilis (sand)	2.5 L ASW (35‰); aerated without replacement	Aquaria (30 × 16 cm) with constant fluorescent illumination	5 wheat grains 1−2 cm^2 fre pieces per ac replenished a
Nitrocra spinipes (sand/muddy sand)	50 mL ASW (35‰); aerated without replacement	Round covered glass dishes (7 × 4 cm) kept in darkness	1 wheat grain p carrot slivers
Schizopera elatensis (sand/gravel)	Same as for *A. subdebilis*	Same as for *A. subdebilis*	Same as for *A.*
Amphiascoides sp. (sand)	100 mL coarse-filtered NSW, heated 10 min at 95°C, and changed weekly	100 mL covered crystallizing dishes	2 cm^2 boiled le
Huntemannia jadensis (sand)	3-mm layer of metazoan-free sand from natural habitat covered by NSW (29‰) and replenished every 2 wk	Petri dishes (3.5 × 1.0 cm) kept under continuous fluorescent illumination	Mixture of pin diatoms deta approx. 20 c natural surfa
Microarthridion littorale (mud)	10 mL Millipore-filtered (0.45 μm) NSW (30‰), 0.1 mL autoclaved resuspended sediments from collection site, and 0.1 mL fresh detrital filtrate (<44 μm) as a bacterial source; 66% of mixture replaced bidaily	Petri dishes (6.0 × 1.5 cm) stored in wet plastic boxes (31 × 24 cm) to minimize evaporation	*Navicula* sp. ar bacteria
Heteropsyllus pseudonunni (muddy sand)	50 mL glass-filtered NSW NSW (13‰) with 50% replaced bimonthly	Erlenmeyer flasks kept in darkness	250 mg dried *J* *roemerianus* to 0.3 mm, 1 L filtered

Food	Inoculation density	Maximum density	Reference
grains and 5 g of cm² fresh lettuce s per aquarium, nished as needed	$17\cdot\text{mL}^{-1}$ (all stages)	$136\cdot\text{mL}^{-1}$ (all stages)	Kahan 1979
grain per dish and t slivers	10 gravids · dish^{-1}	$105 \pm 3.8\cdot\text{mL}^{-1}$ (all stages)	Kahan 1979
s for *A. subdebilis*	$52\cdot\text{mL}^{-1}$ (all stages)	$412 \pm 73\cdot\text{mL}^{-1}$	Kahan et al. 1981
oiled lettuce pieces	$17\cdot\text{mL}^{-1}$ (all stages)	$60-80\cdot\text{mL}^{-1}$ (all stages)	Walker 1979
of pinnate/centric ms detached from ox. 20 cm³ of al surface sand	1 gravid · dish^{-1}	— (attempts at mass culture failed)	Feller 1980
a sp. and incidental ria	— (several gravids and copulating pairs)	—	Palmer and Coull 1980
dried *Juncus* *erianus* stalks ground 3 mm, suspended in iltered NSW for 2 wk	—	— (70% survival of 10 females kept in darkness for 65 d)	Ustach 1982

(1-cm diameter). Vacuum was applied to the flask and pipette via a sink aspirator so that the pipette tip could be used as a wand to draw 25−50% of the flocculent surface sediments and copepods into the flask. Only 25−50% of the surface was removed so that sufficient numbers remained to quickly repopulate a culture. After harvesting, it took approximately 2 wk for *Nitocra* and *Cletocamptus* cultures to regain original densities.

Because the sediments were all <0.125 mm in diameter, they were completely washed through a 0.125-mm sieve leaving only the adults and copepodites to be collected into Petri dishes. Nauplii, early copepodid stages, and very fine sands less than 0.125 mm in size were captured on a 0.63-mm sieve. This sample was not completely free of sediment aggregates, but it was still a very clean sample compared with natural sediments and was much more quickly and efficiently sorted.

Results and Discussion

Five local harpacticoid copepod species were kept in continuous (>6 mo) culture at densities 4−11 times their natural maxima (Table 1). All five are strictly estuarine and live in muddy, detrital-rich sediments. *Nitocra lacustris*, *Cletocamptus deitersi*, *Paronychocamptus huntsmani*, and *Onychocamptus mohammed* are holobenthic, infaunal burrowers and rarely emerge more than 1−2 cm above the sediment surface in natural density cultures. *Scottolana canadensis* is not strictly infaunal but does burrow 1 cm or more to feed and mate. *Nitocra lacustris* and *C. deitersi* are the most prolific and easily maintained harpacticoids cultured thus far, with cultures having a routine longevity of over 12 mo and needing only food, and fresh additions of culture floc every 4−5 mo. *Scottolana canadensis*, *P. huntsmani*, and *O. mohammed* reached considerably lower maximum densities (Table 1) than *N. lacustris* or *C. deitersi*, but they still could be maintained at densities high enough for most laboratory applications (2000−4000 copepods$\cdot$culture^{-1}).

Several mud-inhabiting harpacticoids could not be cultured using these techniques. For example, repeated attempts to culture the tube-building harpacticoid *Pseudostenhelia wellsi* (see Chandler and Fleeger 1984) have failed, as well as single attempts to culture *Enhydrosoma woodini* and *Nannopus palustris*. *Pseudostenhelia wellsi* and *N. palustris* appear to have very specific nutritional requirements not met by this feeding regime, and *E. woodini* has not been collected at densities greater than 30 gravids per collection trip, making it difficult to get a critical inoculation density.

Culture substrates composed of azoic or freshly collected sands and muds have been used by others to culture sediment-dependent harpacticoids but without much success (Table 2). For example, Smol and Heip (1974) found it difficult to locate and count live copepods among sand grains that were at least as large as the copepods themselves, and abandoned its use. Hardy (1978) found that the sand grains and vessel walls of stagnant *Asellopsis intermedia* cultures became quickly overgrown with bacterial films, eventually entrapping and killing the copepods. Techniques for high-density culture of mud-inhabiting meiofauna have also been unsatisfactory, especially within a natural, muddy-sediment substrate. Muddy-sediment particles are much smaller than sands and many are electrically charged. This makes it much more difficult to wash away the organic contaminants that feed dense bacterial blooms without washing away the sediment particles themselves. Only Palmer and Coull (1980) have succeeded in culturing low densities of an epibenthic mud-dweller, *Microarthridion littorale*, in very small amounts of autoclaved mud (Table 2).

Cleaned and sorted muds are better than sands as a culture substrate because all of the sediment particles are less than 0.125 mm. Adult and later-stage copepodites of harpacticoids are usually larger than 0.125 mm; therefore, simple sieving on a 0.125-mm sieve eliminates sediments and the searching and counting problems encountered with natural sands and muds. Most other investigators have grown harpacticoids with no natural substrate and only periodic (daily to monthly) water changes. Therefore, only a few mud-inhabiting harpacticoids have been cultured, and none at the densities achieved using these techniques.

Much more success has come from sediment-free flask, dish, and tank cultivation of epibenthic/fouling (e.g. *Nitocra spinipes* (Kahan 1979)), phytal/demersal (e.g. *Schizopera elatensis* and *Amphiascella subdebilis* (Kahan 1979; Kahan et al. 1981), *Tisbe* spp. and *Tigriopus* spp. (see Kinne 1977 review), and planktonic (*Euterpina acutifrons* (Neunes and Pongolini 1965; Haq 1972)) species. These species do not require a sediment substrate for a place to feed and reproduce, and they have broadly flexible nutritional requirements making them more amenable to batch cultivation. For these reasons, planktonic and semiplanktonic species have been the most commonly used harpacticoids in finfish mariculture (Fujita 1973, 1977).

The key advantages that my culture techniques have over others are that natural, muddy sediments can be sorted (all <0.125 mm), cleansed, and reconstituted to a reasonably life-like sediment structure allowing high harpacticoid densities *without* runaway bacterial growth. A broad-based diet with autotrophic and detrital energy components is provided for the copepods, and a constant influx of fully oxygenated seawater keeps metabolite (and bacterial) accumulation to a minimum. Cultures remain viable for many months with no apparent growth inhibition other than available space. The constant ASW influx may flush out growth inhibiting factors keeping their effects to a minimum (Walker 1979; Fava and Crotti 1979).

The thin-walled, hexagonal culture vessels provide good resolution and multiple angles for direct observation (photography) of behaviors occurring on or below the sediment surface (e.g. see Chandler and Fleeger 1984), and with minimal disturbance to the animals and sediment structure. Such observation is often difficult or impossible in muddy field settings.

The ability to rapidly grow high-density stocks may have potential value for fisheries as larval fish food, or for laboratory studies or population genetics/dynamics, physiology, ecology, toxicology, etc. Mariculture applications would no doubt require larger total numbers of harpacticoids than were cultured here, but fortunately the techniques are simple and inexpensive enough that they probably could be adapted easily to a larger scale.

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Response of Radioactive Trace Metals to Acid–Base Titrations in Controlled Experimental Ecosystems: Evaluation of Transport Parameters for Application to Whole-Lake Radiotracer Experiments[1]

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Radiotracer experiments were carried out in 20 enclosures located in two lakes at the Experimental Lakes Area (ELA), northwestern Ontario, to study pathways of trace metal removal from the water column of shallow lakes. Two removal mechanisms were characterized: (1) sorption to and subsequent transport with falling particles and (2) direct adsorption to surface sediments. Our approach was to measure independently the kinetics of radiotracer sorption, fluxes and concentrations for particles, particle settling velocities, and the "equivalent stagnant boundary film." Our radiotracer results enabled us to test the sensitivity of the tracer removal rates on these rate-determining processes using a numerical transport model. Acid titrations of whole ecosystems revealed that some trace metals (e.g. Mn, Co, and Zn) can diffuse back to the water column as the pH is lowered from 6.5 to 4.8 after 18 d, while others remain tightly bound (e.g. Sn, Fe, Se, Cr, Ag, and Hg isotopes). Subsequent $CaCO_3$ additions to bring back the pH to its original value restored the initial removal conditions for acid-sensitive radiotracers, indicating that the pH sensitivity is reversible. Transport parameters for particle-related pathways or diffusive pathways across the sediment–water interface obtained from our enclosure experiments were used to predict the removal rates of "particle-reactive" ^{60}Co and the "diffusive" pathway tracer ^{134}Cs observed in earlier experiments where radiotracers were added to whole lakes or to larger enclosures.

On a réalisé des expériences avec des traceurs radioactifs dans 20 enclos situés dans deux lacs de la région des lacs expérimentaux (RLE), dans le nord-ouest de l'Ontario, pour étudier les processus de l'élimination dans la colonne d'eau des métaux qui se trouvent à l'état de trace dans les lacs peu profonds. Deux mécanismes d'élimination sont décrits : (1) sorption au niveau des particules qui tombent et transport ultérieur avec ces dernières et (2) adsorption directe au niveau des sédiments de surface. Notre approche consistait à mesurer de façon indépendante la cinétique de la sorption des traceurs radioactifs, les mouvements et les concentrations des particules, les vitesses de sédimentation des particules et la « couche limite inactive équivalente ». Les résultats que nous avons obtenus avec les radiotraceurs nous ont permis de vérifier, en faisant appel au modèle de transport numérique, l'effet qu'ont les taux d'élimination des traceurs sur ces processus qui déterminent les taux. Le dosage à l'acide d'écosystèmes entiers a révélé que certains métaux à l'état de trace (p. ex. Mn, Co, Zn) peuvent retourner dans la colonne d'eau lorsque le pH tombe de 6,5 à 4,8 après 18 j, tandis que d'autres demeurent fortement liés (p. ex. isotopes de Sn, Fe, Se, Cr, Ag et Hg). L'addition ultérieure de $CaCO_3$ pour ramener le pH à sa valeur initiale a rétabli les conditions initiales d'élimination des traceurs radioactifs sensibles à l'acide, ce qui indique que la sensibilité au pH est réversible. On s'est servi des paramètres de transport par biais de particules ou par différents modes de diffusion à travers l'interface sédiment–eau, obtenus à partir des expériences que nous avons réalisées dans des enclos, pour prédire les taux d'élimination de Co^{60} qui réagit avec les particules et le mode de diffusion du traceur radioactif Cs^{134} observé dans des expériences antérieures où l'on a ajouté des radiotraceurs à des lacs entiers ou à des enclos plus gros.

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Our understanding of trace metal geochemistry in lakes is, despite numerous studies, still in its infancy. This is partly due to the geochemical differences between lakes and partly due to the wide variety of aquatic organisms which occur in different lakes. There is evidence that uptake by plankton and subsequent transport by biological debris is the main transport mechanism removing trace metals from lakes (Baccini et al. 1979; Baccini and Joller 1981; Sigg et al. 1982). However, one can also find some evidence that the close proximity to horizontal boundaries affects trace metal distributions, for example by river inputs, by the resuspension of epilimnetic sediments, or by direct sorption reactions at the sediment−water interface (Santschi 1975; Baccini 1976; Leland 1975; Hesslein et al. 1980).

In previous studies, Schindler et al. (1980) and Hesslein et al. (1980) have described results from radiotracer additions to limnocorrals and to whole lakes at the Experimental Lakes Area (ELA), northwestern Ontario. These experiments were designed to study rates and mechanisms of trace metal removal from small lakes. However, while rate constants for the removal of various radioisotopes from the epilimnetic water column could be obtained, the mechanisms could not be constrained well. For some tracers, acidification to pH = 5 in the limnocorral experiments substantially reduced the fraction of the total tracer in the water column that was adsorbed to particles in comparison with control systems at neutral pH. However, no correlation between the rate of tracer removal from the water column and the fraction of tracers adsorbed to particles was found in either the limnocorral or the whole-lake experiments. These observations could not be explained at that time. We therefore carried out a study in the summer of 1981 inside 20 enclosures ("tubes") at the ELA to further constrain the trace metal removal pathways from shallow lakes, and to study the effects of acidification on metal removal pathways in model ecosystems. In such a whole-ecosystem experiment with many interrelated processes it is important to test our understanding of the relevant processes responsible for the tracer movement by using a model simulation of them. A sensivity analysis of the model output on the experimentally determined input parameters is therefore needed. Any interpretation of the chemical processes occurring in such a multireservoir system where tracers injected into one reservoir exchange by both advective and diffusive processes with other reservoirs is dependant on how well we understand those physical transport processes. This is the major emphasis of this paper.

We attempted to answer one important question: how can information gained from small enclosures be applied to whole lakes? We tested the relevance of the two main removal pathways (i.e. scavenging by falling particles and direct sorption at the sediment−water interface) by applying the average parameters determined in the small-enclosure experiments to the results previously obtained when soluble ^{134}Cs (removed mainly at the sediment−water interface) and particle-reactive ^{60}Co (removed mainly by particle scavenging) were added to ELA Lakes 223 (tubes), 224 (whole lake), and 226 (whole lake) (Schindler et al. 1980; Hesslein et al. 1980; R. H. Hesslein, unpubl. data). Radiotracers were removed at the same rates as their stable elements when added simultaneously (e.g. ^{65}Zn, ^{54}Mn, or ^{59}Fe). This will be the subject of a separate paper (Anderson et al. 1982; and unpubl. data).

Materials and Methods

The tubes used for these experiments were constructed of

TABLE 1. Experimental conditions inside L-114 and L-302S tubes which received radiotracer additions.

Characterization or parameter	L-302S	L-114	L-302S tubes 1	2	3	8	9	Avg. 1−3	12	13	L-114 tubes 14	15	16	17	18	19	20	Avg. 14−20
Open/closed bottom	—	—	Op	Op	Op	Cl	Cl		Cl	Cl	Op	Op	Op	Op	Op	Op	Op	
Treatment[a]	—	—	C	C	N	S(302)	S(114)		C	C	Fe	Mn	Zn	K	N	C	C	
mmol HCl added (day 18−37)	—	—	106	72	159	89	52.5		—	80	101	87	93	72	119	0	75	
mmol $CaCO_3$ added (day 37−62)	—	—	53	—	80	—	—		—	—	—	—	46	—	—	—	—	
pH (day 0−18)	6.8	6.3	6.8	6.9	9.0	6.5	6.8		—	7.0	6.6	6.6	6.8	6.5	9.2	6.6	6.6	
pH (day 17−37)	6.8	6.3	4.7	4.7	4.7	4.7	4.7		—	4.3	4.8	4.8	4.8	4.8	4.8	5.8	4.7	
pH (day 37−62)	6.6	6.2	7.3	4.8	8.7	4.7	4.6		—	4.2	4.7	4.7	6.5	4.7	4.7	5.7	4.7	
F = particle flux (10^{-5} $g \cdot cm^{-2} \cdot d^{-1}$)	—	—	5	8	11	15	20	8	—	5	12	13	20	10	19.5	18	12	15
P = particulate matter concn. ($mg \cdot L^{-1}$)	2	4	2.5	1.8	2.5	8	6.7	2.3	—	4	6	4	6	2.5	5	5.5	5	4.9
S = settling velocity ($cm \cdot d^{-1}$)	—	—	20	44	44	20	30	35	—	12.5	20	32.5	33	40	38	30	24	30
Primary productivity ($mg\ C \cdot m^{-3} \cdot d^{-1}$)																		
1 d prior to tracer additions	128	534	150	—	—	—	—	—	110	—	750	—	—	—	—	—	—	—
day 13	75	268	57	—	60	—	—	—	54	—	150	—	—	—	—	—	—	—
Chlorophyll a ($\mu g \cdot L^{-1}$)	2.1	5.9	2.6	3.7	14→44	—	—			2.5	5.9	—	—	—	32→18	—	—	
Porosity of surface sediments (0−2 cm)	0.7	0.98	0.75	0.6	—	—	—	0.7	—	0.98	0.98	0.98	0.98	0.98	0.98	0.98	0.98	0.98

[a] C = control tube, N = nutrient additions of 200 μg PO_4-$P \cdot L^{-1}$ and 750 μg NO_3-$N \cdot L^{-1}$, S = sediment slurry from lake indicated in parentheses, trace metals: 100 μg $Fe^{3+} \cdot L^{-1}$, 140 μg $Mn^{2+} \cdot L^{-1}$, 50 μg $Zn^{2+} \cdot L^{-1}$, 13 mg $K^{+} \cdot L^{-1}$.

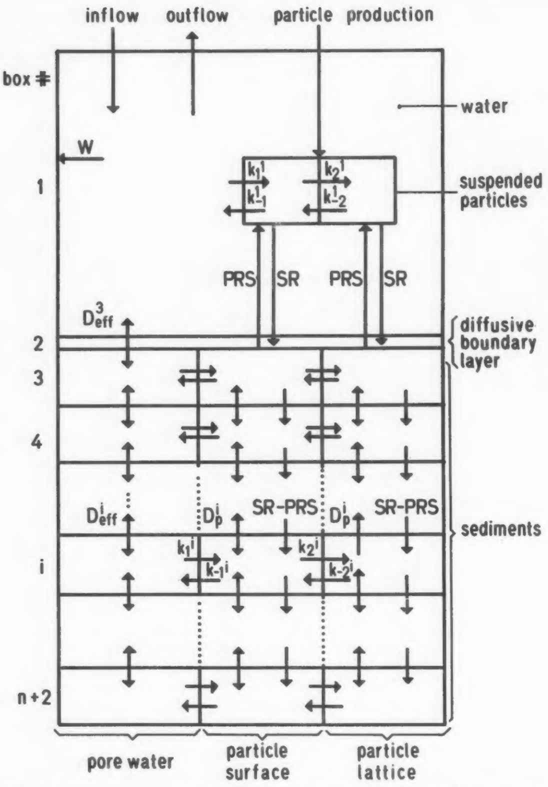


FIG. 1. Schematic representation of the physical transport processes included in the numerical transport model. Details of the model are presented in Nyffeler et al. (1986). The system is divided vertically into a series of boxes which include a well-mixed water column (1), the diffusive boundary layer (2), and a number of layers of sediments ($i = 3$ to $n + 2$). The system is divided horizontally into compartments that represent tracers which are in solution, adsorbed to particle surfaces, or incorporated into solid matrices. k_1 and k_{-1} are adsorption and desorption rate constants, k_2 and k_{-2} are rate constants for transport into or out of solid matrices, D_{eff}^i and D_p^i are the pore water diffusion and sediment mixing rate constants, respectively, and W, PRS, and SR represent wall adsorption, particle resuspension, and particle settling rates, respectively.

nylon-reinforced polyethylene. The top of each tube was held in a 1-m-diameter ring of plastic pipe attached to a wooden frame held 30 cm above the air−water interface by styrofoam floats. The bottom of each tube was embedded in the sediments. The experiments started in July 1981.

Two lakes were chosen for this work to provide contrasting sediment characteristics. Lake 302S is a typical oligotrophic Canadian shield lake (mean depth = 5 m) with quartz−plagioclase sandy sediments covered by a thin organic-rich flocculent layer. Lake 114 is a shallow (mean depth = 1.7 m) dystrophic lake with highly porous, flocculent, organic-rich sediments. Table 1 gives a summary of the experimental conditions inside selected tubes of a total of 20 plastic tubes, each about 1.2 m deep, which were deployed in ELA Lakes 114 and 302S. In short, they consist of duplicate control tubes in each lake with their bottoms open to the sediments, one open bottom tube in each lake receiving nutrient additions (raising the initial concentrations of PO_4-P from 5 (TDP) to 200 $\mu g \cdot L^{-1}$, and NO_3-N from 1 to 75 $\mu g \cdot L^{-1}$) and four tubes in L-114 receiving the additions of either 50 µg $Zn^{2+} \cdot L^{-1}$, 140 µg $Mn^{2+} \cdot L^{-1}$, 100 µg $Fe^{3+} \cdot L^{-1}$, or 13 mg $K^+ \cdot L^{-1}$. Several closed-bottom tubes were set out in L-302S: two were used for the study of particle adsorption in the absence of a sediment phase; one contained a 5-cm-deep layer of sand precleaned with H_2O_2; five tubes contained a layer of natural sediments about 5 cm deep, one each from L-114, L-302S, and three other lakes; and one contained a gypsum plate for determining the equivalent boundary layer thickness (tube 12). One additional tube was used for experimentation with zooplankton to test the rate of tracer incorporation into fecal pellets.

TABLE 2. Model parameters and the techniques to measure them.

Parameter	Measurement techniques
Settling velocity of particles (V_p)	Measurement of particle flux (F) by cylindrical sediment traps (6.6-cm width and 30-cm height) and particle concentrations (C_p) by 0.45-µm Nuclepore filtration: $V_p = F/C_p$
Adsorption/desorption rate constants ($^*k_1$, k_{-1}) on sediment and/or suspended particles	Measurement of the adsorption rate on particles in laboratory batch experiments (Nyffeler et al. 1984) at concentrations of ~100 $mg \cdot L^{-1}$ for sediments, and in situ K_D (t) values calculated from sediment trap material for suspended particles
Stagnant boundary film thickness (z)	Measurement of the dissolution rate of gypsum resting near the sediment−water interface or by model fitting the removal of ^{134}Cs (Santschi et al. 1983)
Benthic mixing rates (D_B)	Measurement of the radiotracer penetration into the sediments or by model fitting the removal of ^{134}Cs to the sediments

We chose, for this work, a suite of radiotracers which exhibit a wide range of chemical reactivities with respect to adsorption to particles. Our objective was then to use selected tracers with known particle reactivities to evaluate individual physical transport parameters which control the removal of trace metals from lakes. Approximately 1×10^6 to 3×10^6 Bq of gamma-emitting ^{113}Sn (IV), ^{59}Fe (III), ^{60}Co (II), ^{57}Co (III), ^{58}(Co (II) humic acid complex), ^{54}Mn (II), ^{65}Zn (II), ^{75}Se (IV), ^{134}Cs (I), ^{203}Hg (II), ^{51}Cr (III), ^{51}Cr (VI), ^{22}Na (I), and ^{110m}Ag (I), dissolved in small amounts (microlitres) of HCl or HNO_3, were added individually to selected or all of the tubes. Oxidation states of the tracers at the time they were added to the tubes are given in parentheses. At one extreme is ^{22}Na which sorbs only weakly to particles and is found mostly in the aqueous phase in natural water systems. At the other extreme we have used the so-called "particle-reactive" nuclides ^{59}Fe and ^{113}Sn (Santschi et al. 1980) as well as ^{60}Co and ^{54}Mn, which also sorb readily to suspended particles in natural waters (Nyffeler et al. 1984). ^{65}Zn and ^{134}Cs have intermediate affinity for adsorption to biogenic and silicate particles.

Water samples of 100 and 250 mL, integrated over the water column by a 1-m-long tube, were collected routinely to monitor the total, particulate, and dissolved tracer activities (after filtration through prewashed and preweighed 0.4-µm Nuclepore filters) and to provide the concentration of suspended par-

TABLE 3. Kinetic constants and K_D (L-114).

	Batch technique (sediment[a])						In situ K_D^∞ (filtered or trapped particles)	
	pH = 6.5			pH = 4.3				
Isotope	$*k_1$ ($cm^3 \cdot g^{-1} \cdot d^{-1}$)	k_{-1} (d^{-1})	K_D^∞ ($cm^3 \cdot g^{-1}$)	$*k_1$ ($cm^3 \cdot g^{-1} \cdot d^{-1}$)	k_{-1} (d^{-1})	K_D^∞ ($cm^3 \cdot g^{-1}$)	pH = 6.5	pH = 4.8
^{54}Mn	1×10^4	0.1	1×10^5	2.3×10^2	1	2.2×10^2	1.3×10^6	1×10^3
^{60}Co	1.3×10^4	0.1	1.3×10^5	7×10^2	1	7×10^2	1×10^6	4×10^3
^{113}Sn	4.5×10^4	0.3	1.3×10^5	8×10^5	1	8×10^5	1×10^6	5×10^4
^{110m}Ag	6×10^3	0.3	2×10^4	7×10^4	1	7×10^4	7×10^4	2×10^4
^{59}Fe	4×10^4	0.4	1×10^5	7.5×10^4	1	7.5×10^4	1×10^6	1.5×10^5
^{65}Zn	3.8×10^4	0.5	7.5×10^4	1.8×10^3	1	1.8×10^3	7×10^4	5×10^3
^{134}Cs	1.5×10^4	2	7.5×10^3	1.5×10^4	2	7.5×10^3	5×10^3	5×10^3
^{203}Hg	1.1×10^3	1	1.1×10^3	6×10^4	1	6×10^4	1×10^5	9×10^4
^{75}Se	1.2×10^4	1	1.2×10^4	3.5×10^4	1	3.5×10^4	5×10^4	7×10^3
^{51}Cr(III)	2.1×10^3	1	2.1×10^3	3.1×10^4	1	3.1×10^4	3×10^5	6×10^4
^{51}Cr(VI)	—	—	—	—	—	—	7×10^4	2×10^4
^{22}Na	—	—	44	—	—	44	—	—
^{125}Sb	68	1	68	—	—	—	—	—

[a]Sediments consists of 50% organic matter and 50% silicates. Cation exchange capacity (tritium technique): 4.60 (moles of sites $\cdot$ kg^{-1}).

TABLE 4. Comparison of K_D^∞ values in L-302S (Rate constants for sorption reactions with L-302S sediments could not be determined from the available samples).

	Sediments with batch technique[a]		Suspended particles (in situ)	
Isotope	pH = 6.5	pH = 4.3	pH = 6.5	pH = 4.8
^{54}Mn	7×10^4	1.1×10^2	1.5×10^5	7×10^3
^{60}Co	1.1×10^5	9×10^2	2×10^6	2×10^3
^{113}Sn	5×10^4	8×10^4	1.5×10^6	1×10^6
^{59}Fe	5×10^4	7×10^3	1×10^6	2×10^4
^{65}Zn	6×10^3	2×10^2	1×10^5	6×10^3
^{134}Cs	5×10^3	1.4×10^3	1×10^4	1×10^4
^{110m}Ag	5×10^3	4.4×10^3	2×10^5	2×10^5
^{203}Hg	5×10^2	9×10^3	3×10^5	3×10^5
^{75}Se	4×10^3	6×10^3	1×10^5	1×10^4
^{51}Cr(III)	7×10^3	6×10^3	4×10^5	2×10^5
^{51}Cr(VI)	—	—	1.4×10^5	2×10^4
^{22}Na	3	3	—	—
^{125}Sb	1×10^2	8×10^2	—	—
^{57}Co(III)	—	—	2×10^6	1×10^4
^{58}Co(-humics)	—	—	7.5×10^5	6×10^3

[a]Sediments consist mainly of sand with a few percent organic matter or clay. Cation exchange capacity (tritium exchange technique): 0.12 (moles of sites $\cdot$ kg^{-1}).

ticulate matter. Water samples and filters were gamma counted on a Ge(Li) detector coupled to a 4096 channel pulse height analyzer. Appropriate geometry factors were determined by counting mixed isotopic standards in the same geometry configurations as were used for the samples. Sediment traps, made out of 1000-mL plastic cylinders of 34.5 cm^2 surface area and 29 cm height, were used in all tubes and sampled initially daily, and subsequently at longer time intervals. To some of the traps we added 4 g of NaCl to test its effectiveness as a preservative. Periodically, primary productivity (Fee 1973), nutrients, O_2, zooplankton abundance, chlorophyll *a*, pH, and temperature were monitored. After 18 d, HCl was added to selected tubes to lower the pH to 4.8. The pH was monitored daily, and acid was added as necessary to maintain a pH of 4.8. A total of 50−160 mmol of HCl was added to each tube during

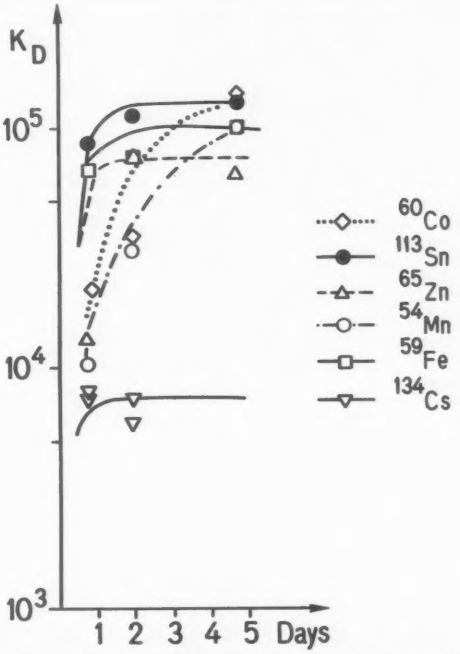


FIG. 2. Rate of uptake of selected radioactive tracers on sediments of L-114 (at $C_p \cong 100$ mg $\cdot$ L^{-1}) in laboratory batch experiments, at 20°C, shown as the ratio of particulate to soluble activity (K_D) versus time. One standard deviation from radioactive counting amounts to about 1−5%. The parameters ($*k_1$, k_{-1}) used in the model fits (solid and broken lines) are given in Table 3. They can be considered approximate only due to the limited data base. K_D is related to the rate constants for adsorption (k_1*) and desorption (k_1) and to the particle concentration (C_p) by

$$K_D(t) = [1 - \exp((-k_1* + k_{-1})t)]/\{[\exp(-(k_1* + k_{-1})t) + k_{-1}/k_1*]C_p\}.$$

$$k_1 = *k_1 \times C_p$$

For ^{134}Cs, the model curve is given by data sets from similar lake sediments (not shown), which took 1 d to reach an equilibrium distribution.

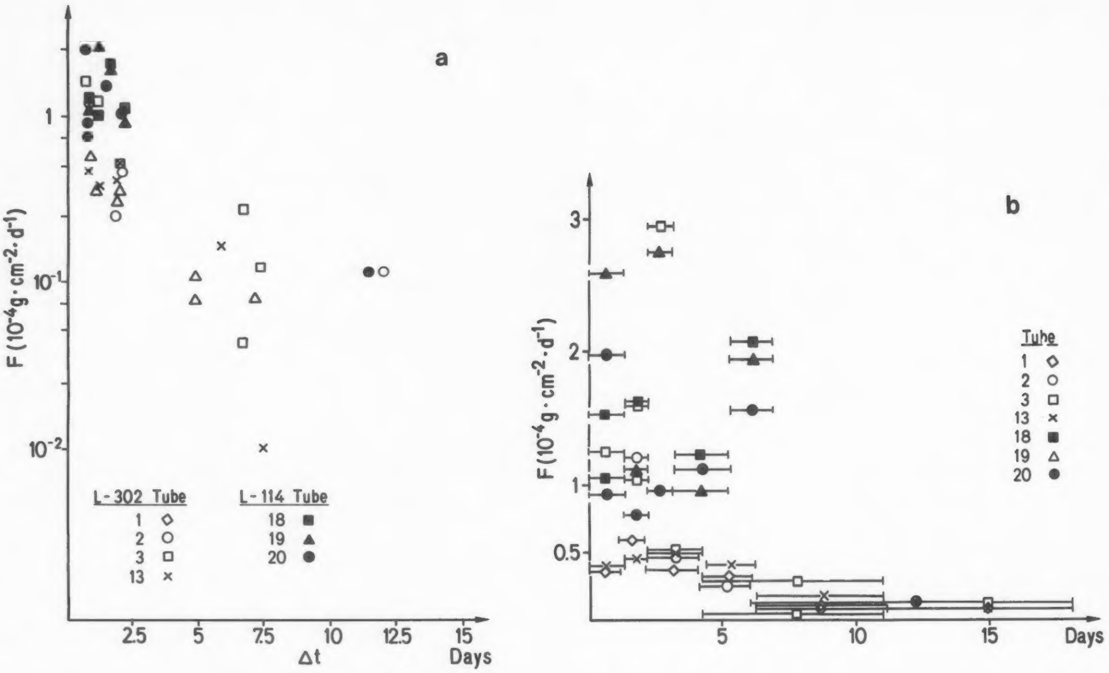


FIG. 3. Particle flux (*F*), as measured with sediment traps, given as function of (a) exposure time (Δt) and (b) time into the experiment, where the exposure time is given by the width of the bars. The decrease of the flux is intepreted as indicating the remineralization or grazing by zooplankton of particles caught in the sediment traps (see text).

the acidification phase. After 37 d an equivalent amount of $CaCO_3$ was added to selected tubes to bring the pH back to its initial value between 6.5 and 7.0 (Table 1). These amounts of acid and $CaCO_3$ are high enough to ensure that the surface layer sediments, to which most of the tracers had been removed by day 18, were also held at the given pH. It does not matter that the pH is higher at greater depths in the sediments because it is only a 1- to 2-cm-deep layer of surface sediments that exchanges metals with the water column.

In separate experiments, the kinetics of radiotracer sorption to sediment particles were studied using the methods described in Nyffeler et al. (1984). Approximately 10 mg of surface sediments was shaken with 100 mL of lake water which contained a mixture of radioisotope spikes. Periodically, samples were filtered and gamma counted. Sorption kinetics were then modelled from the partitioning of the tracers between dissolved and particulate phases as a function of time (Nyfeller et al. 1984).

Numerical Transport Model

Our approach to the modelling of radiotracer cycling in these controlled experimental ecosystems was to (1) measure independently the transfer coefficients for trace metal transport by adsorption to settling particles and to surface sediments, (2) measure the kinetics of radiotracer sorption onto particulate matter, (3) measure and/or model the rate of sediment mixing, and (4) evaluate the sensitivity of each removal pathway to each of the stated parameters by modelling the removal of soluble and particle-reactive radiotracers from the water column to the sediments, and the return of certain tracers to the water column (back diffusion) after acidification of the enclosed systems.

The numerical transport model used to model points 3−5 is described in Nyffeler et al. (1986). In short, it consists of a number of boxes between which each tracer is transported (Fig. 1). The tracer starts out in a well-mixed water column, separated from the sediments by a thin stagnant film (also referred to as the diffusive sublayer), through which dissolved species pass by molecular diffusion. The tracer is allowed to adsorb to freshly produced particles falling through the water column or, after diffusing through the stagnant film, to particles in the sediments. The tracer in the sediments exchanges between pore water and solids, which are allowed to be mixed vertically. The model also allows for (1) the transfer of the tracer from exchangeable surface sites to immobile lattice positions, (2) particle resuspension, (3) time variable inputs for volumes, sediment surface areas, particle fluxes, and the settling velocities of particles, and (4) depth variable porosities and benthic mixing rates. Acid titrations of whole water columns are handled by changing the adsorption and desorption rate constants to those measured at lower pH. Some of the model parameters which were determined in separate experiments could also be derived by fitting the removal and back diffusion curves. A list of model parameters and the means by which they were measured are given in Table 2.

Results and Discussion

Mechanisms Removing Radiotracers from the Epilimnetic Water Column

Radiotracers can generally be removed from lake water in the tubes by three different mechanisms: (1) they can absorb to,

TABLE 5. Comparison of K_D^∞ ($cm^3 \cdot g^{-1}$) of selected isotopes on filtered particles or particles caught in sediment traps.

		Tube					
Isotope	Material[a]	1	2	3	13	19	20
^{60}Co	F	3×10^6	1.5×10^6	8×10^5	1×10^6	8×10^5	1×10^6
	ST	3×10^6	1×10^6	1.5×10^6	1.5×10^6	1×10^6	1.5×10^6
^{54}Mn	F	2×10^6	1.5×10^6	1.2×10^6	1.5×10^6	1.1×10^6	1×10^6
	ST	2×10^6	1×10^6	1.5×10^6	1×10^6	1.3×10^6	1.5×10^6
^{59}Fe	F	1×10^6	1.5×10^6	1×10^6	7.5×10^5	1×10^6	1×10^6
	ST	1.2×10^6	8×10^5	6×10^5	8×10^5	8×10^5	1×10^6
^{113}Sn	F	2×10^6	—	—	—	1×10^6	—
	ST	1.5×10^6	—	—	—	8.5×10^5	—
^{65}Zn	F	1×10^5	8×10^4	1.5×10^5	6×10^4	4.7×10^4	5×10^4
	ST	1.5×10^5	6×10^4	1.5×10^5	9×10^4	5×10^4	5×10^4

[a] F = filtered particles, ST = particles from sediment types.

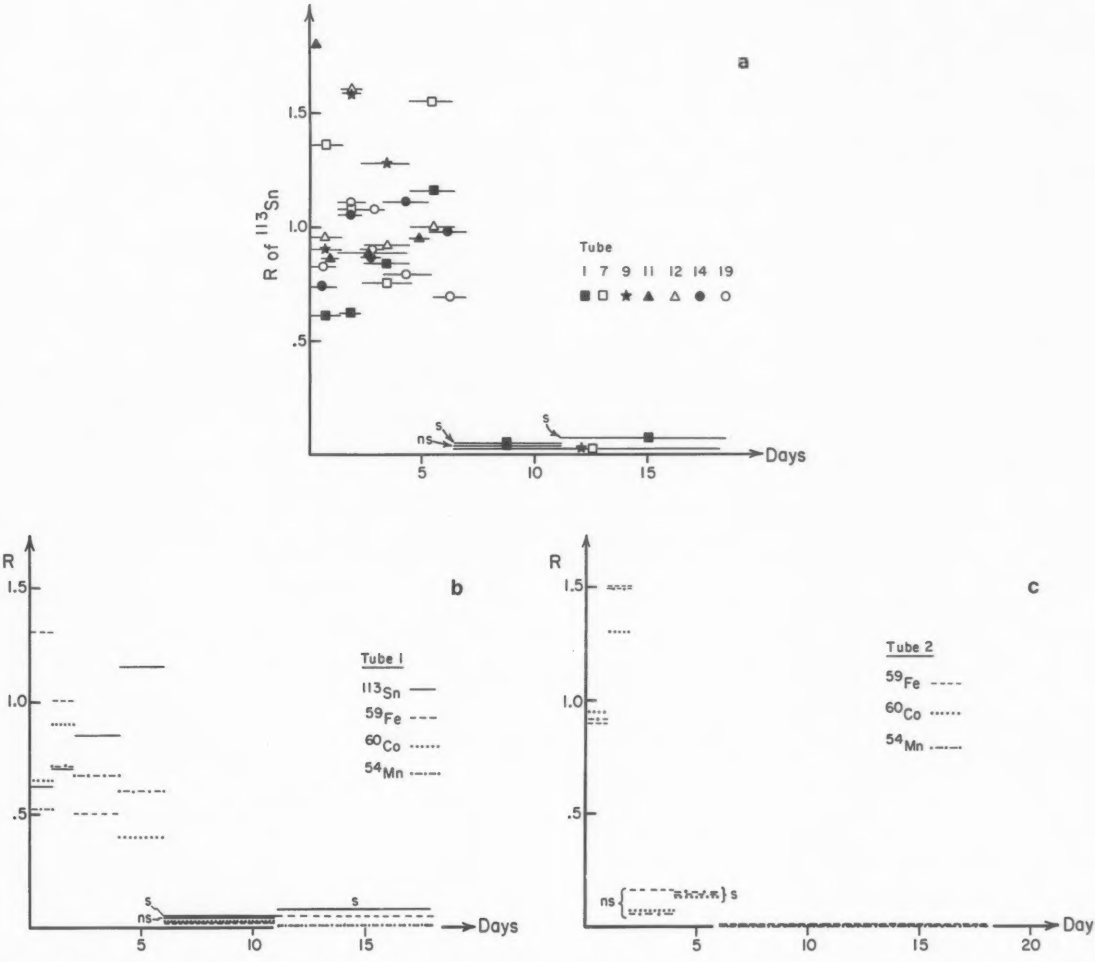


FIG. 4. Ratio (R) of the radioisotope flux (as measured with sediment traps) to the total removal flux (as calculated from the differences in total concentrations during deployments) plotted versus time of the experiment, where the exposure time is given by the width of the bars. (a) ^{113}Sn in tubes from L-114 and L-302S; (b) ^{113}Sn, ^{59}Fe, ^{60}Co, and ^{54}Mn in tube 1; (c) ^{59}Fe, ^{60}Co, and ^{54}Mn in tube 2. ns = no salt added, s = salt added. The scatter of the data is the result of the uncertainty in the estimation of the radioisotope flux from the water column during the short deployment times. The decrease of the amount of the tracers found in the traps as compared with that expected from the decrease of the water column activity is interpreted as indicating the release of the tracers associated with the remineralized or grazed particles in the sediment traps.

TABLE 6. Comparison of equivalent boundary film thicknesses z.

System	Gypsum dissolution rate ($mg \cdot cm^{-2} \cdot d^{-1}$)	z (cm)		
		$CaSO_4 \cdot 2H_2O$ diss.	^{134}Cs removal	^{65}Zn removal
Tubes 1–3 (L-302S)	—	—	0.1–0.2	0.06
Tube 10 (L-302S)[a]	11.4	0.17	—	—
Tubes 14–20 (L-114)	—	—	0.05	0.03
L-302S				
1981	17.0	0.11±0.005[b]	—	
1982	16.7	0.12±0.005[b]	—	—
L-226NE	14.9	0.13[b]	0.075±0.025	—
L-226SW	23.5	0.08[b]	0.075±0.025	—
L-223	11.5	0.16[b]	0.075±0.025	—
L-224	13.3	0.14[b]	0.075±0.025	—
L-114	12.8	0.14[b]	—	—

[a] z was calculated from the increase in Ca^{2+} concentration from 2.3 to 9 ppm in 18 d, volume $\cong 1 \ m^3$, surface area of gypsum = 136 cm^2.

[b] These are upper limits, as the plates outside the tubes were approximately 50% covered with sediment particles at the end of the deployment; z was calculated from the weight loss per unit area and time (F) as follows:

$$F = \frac{D \cdot (C_s - C)}{(z)(0.23)}$$

where D = molecular diffusion coefficient of Ca^{2+}, SO_4^{2-} pair at 22.5°C ($8.6 \times 10^{-6} \cdot cm^{-2} \cdot s^{-1}$), C_s = Ca^{2+} concentration at saturation (=608 ppm), and C = in situ concentration of Ca^{2+} (=2 ppm). The factor 0.23 converts from the atomic weight of gypsum to that of Ca^{2+}.

or be taken up, by suspended particles (composed here mostly of plankton) and subsequently settle to the bottom of the tubes, (2) they can absorb directly to sediments after diffusion through a stagnant film (diffusive sublayer) overlaying the sediments, or (3) they can absorb to the walls of the container. Pieces of wall material exposed to the radioisotopes in the enclosures over the course of the experiment were gamma counted to assess the third possibility and yielded negligible wall adsorption (i.e. ≤5% of the total removal, see section on mass balance). This leaves only pathways 1 and 2 to be considered seriously and the initial removal rate constant (λ_i) contains two components: λ_s for removal by settling particles and λ_D for direct sediment uptake, where $\lambda_i = \lambda_s + \lambda_D$. In the following sections, we will discuss the different mechanisms separately.

Rate Constants for Adsorption and Desorption

Figure 2 shows the results from the laboratory batch experiments in which the ratio of the radiotracer activity on sediment particles to the activity in solution (K_D) is plotted as a function of time. Radioisotope sorption at near-natural levels of suspended particles takes several days to reach equilibrium (Nyffeler et al. 1984). Strictly, 5 d was insufficient time to observe constant radiotracer distributions between particles and solution. However, based on our sediment trap data, the particle residence time in a 1-m water column is normally less than 5 d. Thus, an empirical description of sorption reactions over that time period is more appropriate than assuming a constant K_D. Also shown in Fig. 2 are model fits to the data using the approach described in Nyffeler et al. (1984). The appropriate rate constants for adsorption–desorption reactions at two different pH levels (6.5 and 4.3) are given in Table 3. Since the data points do not quite adequately constrain the model curves, the estimates of rate constants $*k_1$ and k_{-1} have uncertainties of a factor of ±2. The values for $K_D^{\infty} = *k_1/k_{-1}$ at pH 4.3 for some radioisotopes are considerably lower than at pH 6.5 (Tables 3 and 4), suggesting that these radioisotopes exist as cationic species (Li 1981). Some isotopes (such as ^{113}Sn, ^{59}Fe, ^{51}Cr, ^{203}Hg, ^{75}Se), however, have similar K_D values at both pH 6.5 and 4.3, suggesting either that they exist as anionic or neutrally charged species in lake water or that reducing the pH does not increase the solubility of solid phases, such as humates, which incorporate some of these tracers.

Several days were required to reach an adsorption–desorption equilibrium in situ (i.e. a constant K_D value calculated from particulate/dissolved activity ratios in the tubes) in L-114, whereas less than 1 d was required in L-302S. For both lakes, and for most radiotracers, rate constants for adsorption to particles were higher in situ than in laboratory experiments where surface sediments were used. More importantly, the K_D values obtained in laboratory experiments do not agree very well for many radionuclides with the in situ determination of K_D using particles collected either with sediment traps or by filtration. However, K_D values obtained by the latter two in situ techniques are in good agreement (Table 5). For the more soluble radiotracers such as ^{134}Cs and ^{65}Zn, the agreement between laboratory and in situ K_D values is good (Tables 3 and 4). For the particle-reactive tracers such as ^{113}Sn, ^{59}Fe, ^{54}Mn, and ^{60}Co, they disagree by an order of magnitude (Tables 3 and 4). The difference appears to be mainly due to the fact that we did not reach equilibrium distribution in the batch experiments. The slower uptake kinetics observed in the laboratory experiments may in turn be related to compositional differences between the two types of particles: the in situ particles contain live plankton and much less degraded organic detritus than the surface sediments. Consequently, in these systems, in situ determinations of K_D rather than the results from the laboratory experiments must be used for modelling the radiotracer sorption in the water column.

Particle Fluxes and Settling Velocities

In order to minimize decomposition of detritus collected in the sediment traps, exposure times were kept as short as possible. Particle fluxes in the traps from different tubes are plotted versus deployment times in Fig. 3a. Some resuspension of surface sediment may initially have occurred in some tubes, since particle fluxes estimated from trap deployments are sometimes larger than rates of new particle formation by primary production (by 100% or more, Table 1). Traps deployed for longer than 2 d caught significantly less material per day than those deployed for 1−2 d. Since the longer trap deployments tended to occur later in the experiment (Fig. 3b), we must demonstrate that the lower apparent fluxes in the longer deployments result from a loss of material from the traps rather than from a decreasing particle flux with time. For that reason, the ratio of the flux of ^{113}Sn (a strongly particle-reactive tracer) collected in the traps to the total removal flux of ^{113}Sn calculated from the decrease in its water column concentration during the trap deployment (R) is plotted versus experimental time for several tubes in Fig. 4a and compared with results for other nuclides in tube 1 in Fig. 4b. Traps deployed 5 d or longer caught significantly less than 10% of the expected ^{113}Sn fluxes whereas traps deployed for 1−2 d collected ^{113}Sn fluxes that nearly balanced the total removal rate. Similar results were obtained for the other tracers in tube 1 (Fig. 4b). Uncertainties in our estimates of tracer removal during the short sediment trap deployments cause errors in R of ±30%, but certainly cannot account for R values less than 0.1. The addition of 5% NaCl did not protect particles from zooplankton grazing or bacterial degradation during the 5- to 12-d deployments (Fig. 4a−4c). Consequently, trap fluxes can only be used when exposure times are less than 2 d.

Average settling velocities of particles (V_p) can be calculated from the particle flux (F) and the particulate matter concentration (C_p) as $V_p = F/C_p$. Average values obtained for both L-302S and L-114 were around 30 cm·d^{-1}.

Incorporation of radionuclides into fecal pellets accounted for only a few percent of the water column removal of the tracers. This was determined in separate experiments in which zooplankton collected by plankton tows in L-302S were enclosed in a cage in one of the tubes and the fecal pellets collected and gamma counted.

The importance of uptake by suspended particles can be tested also in tubes 12 and 13, which had closed bottoms and did not contain any sediments. The rate constant for removal of an isotope by particles (λ_s) is a function of F, C_p, the mean depth (h), and the fraction of the tracer associated with suspended particles (f_p) as follows:

(1) $\lambda_s = F \cdot f_p/(C_p \cdot h) = V_p \cdot f_p/(h)$

with $V_p = F/C_p$ = mean settling velocity of particles. In tube 13, V_p was 12 cm·d^{-1}. We can express f_p as a function of the K_D at time t and of C_p as

(2) $f_p = K_D(t) \cdot C_p/(1 + K_D(t) \cdot C_p)$.

Particle-reactive isotopes such as ^{113}Sn, ^{59}Fe, ^{60}Co, and ^{54}Mn were measured to be 80−90% associated with particles in tubes 12 and 13, consistent with their in situ K_D values measured in other tubes of (1.3 ± 0.5) × 10^6 (Table 5). Therefore, we can use these isotopes to evaluate the importance of removal by settling particles. Given these values of V_p, f_p, and K_D, we calculate a λ_s of 0.085·d^{-1} (equation 3), or a half removal time $t_{1/2} = \ln 2/\lambda_s$ of 8 d, consistent with the observations (see Fig. 8). This consistency between the rate of removal by adsorption to settling particles calculated using the various transport parameters and the total removal rate, which can only occur by adsorption to settling particles in tubes 12 and 13, assures us that we have properly evaluated the transport parameters related to particle removal.

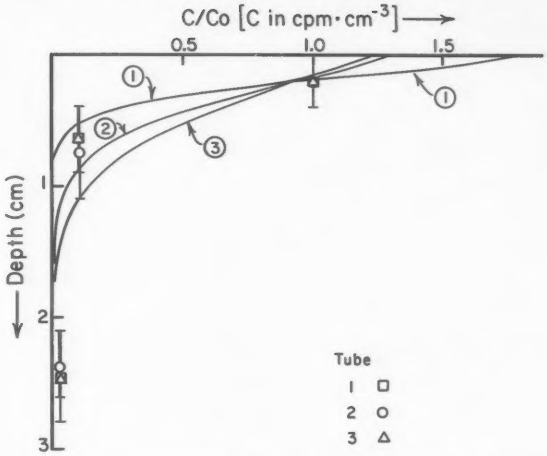


FIG. 5. Penetration of radioisotopes into surface sediments of L-302S tubes 1−3 after 16 d (1981) compared with model predictions using the measured rates of radioisotope removal from the tube water columns as input functions. Model run 1 uses a sediment mixing coefficient of 8 × 10^{-8} cm^2·s^{-1}, run 2 uses 3 × 10^{-7} cm^2·s^{-1}, and run 3 uses 5 × 10^{-7} cm^2·s^{-1}.

Resistance to Chemical Transport Across the Sediment−Water Interface

The transfer coefficient for uptake of radiotracers by adsorption to surface sediments can be expressed as D/z (D = molecular diffusion coefficient and z = diffusive sublayer or "stagnant boundary film" thickness). The equivalent thickness of a stagnant boundary film overlying the sediments (z) was determined by two methods. The first estimate of z was obtained by measuring the weight loss of flat gypsum plates imbedded into PVC holders resting on the sediment−water interface for 1−2 wk (Santschi et al. 1983), which gave values of 0.1−0.2 cm (Table 6). The rates at which the more soluble tracers such as ^{134}Cs and ^{65}Zn are initially removed from the water column provide a second means of calculating z. Initially, adsorption to the sediments is rapid and desorption is negligible. Hence, the rate limiting step for removal from the water column is diffusion of the tracer through the boundary film. Removal is initially first order ($dC/dt = -\lambda_i \cdot C$), where the initial removal rate constant λ_i, which is valid for maximum concentration gradients between water and sediment pore waters, is a function of the film thickness z as follows (Santschi et al. 1983):

(3) $\lambda_i = [D_m \cdot A/(z \cdot V)]\,(1 - f_p)\lambda_{\text{SWI}}$

where D_m = molecular diffusion coefficient (square centimetres per day), f_p = fraction of the tracer in the water column adsorbed to particles ($f_p \ll 1$ for soluble tracers), A = area

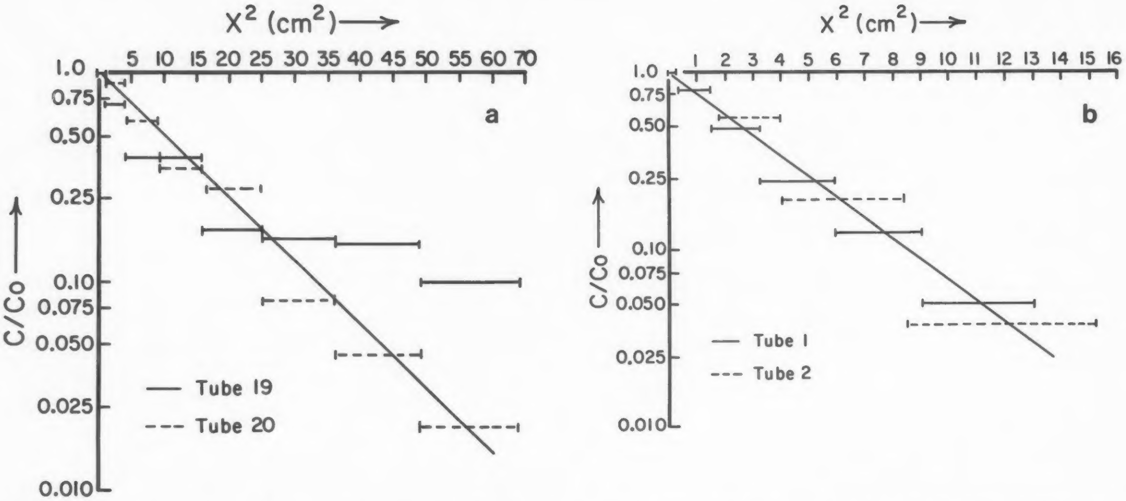


FIG. 6. Normalized activities of ^{60}Co in surface sediments of (a) L-114 tubes 19 and 20 and (b) L-302S tubes 1 and 2 after 398 d (1982) plotted as a function of depth squared (x^2). The slope is proportional to the particle mixing coefficient D_B (equation 4). Similar profiles could be obtained for ^{113}Sn and ^{54}Mn. Sediment mixing coefficients calculated using equation 4 are 1×10^{-7} cm$^2 \cdot$s^{-1} for tubes 19 and 20 and 2.5×10^{-8} cm$^2 \cdot$s^{-1} for tubes 1 and 2.

(square centimetres) of exposed sediments, and V = volume (cubic centimetres) of water in the tube. Values of λ_i for ^{134}Cs in L-302S in L-114 tubes range from 0.10 to 0.14$\cdot$d^{-1}. Using $D_m = 1.96 \times 10^{-5}$ cm$^2 \cdot$s^{-1} and V/A = 125 cm, one can estimate z = 0.1–0.14 cm, very close to the values of z obtained independently from the gypsum dissolution method (Table 6).

These estimates of z are averages which apply only to time scales of more than 1 d, since water mixing, which determines the magnitude of z, is predominantly driven by heating at the sediment–water interface during the day, by convective cooling of water during the night, and by occasional wind-driven circulation in these shallow lakes.

The parameters relevant to removal by direct sediment uptake include not only z, but also the kinetics of tracer adsorption onto sediment particles ($^*k_1$ and k_{-1}), which determines the value of f_p at any given time, and the benthic mixing rate constant (D_B).

Initially, adsorption to the sediments is rapid and desorption is negligible. Hence, the rate limiting step for removal from the water column is diffusion of the tracer through the boundary film. Thus, the initial removal rate λ_i is controlled by D_m/z (equation 3).

Eventually, the concentration of tracer adsorbed to the surface sediments builds up and desorption becomes a significant process. Desorption will become significant at a different time for each element, depending on the magnitudes of $^*k_1$ and k_{-1}. As the surface sediments approach an adsorption–desorption equilibrium with the surrounding water, the concentration gradient across z no longer limits transport of the tracer to the sediments. Removal then becomes limited by the rate of tracer penetration deeper into the sediments. Penetration occurs both by molecular diffusion of the tracer in solution and by physical and/or biological mixing of the sediments which causes tracer-laden surface sediments to be buried and tracer-free deep material to be brought to the sediment–water interface where it then adsorbs additional tracer from the water column. The rate of sediment mixing (D_B) is thus the dominant parameter controlling tracer removal during later stages of the experiment. Since penetration into the sediments is a slower process than diffusion across z, removal of the more soluble tracers tends to slow down with time (see Fig. 7a and 9a). This feature is not seen for every quasi-conservative tracer as clearly as for ^{134}Cs because acidification on day 18 caused other tracers, for which we would eventually have seen this effect (e.g. ^{65}Zn), to be remobilized from the sediments.

Mixing Rates in the Sediments

Sediment profiles of particle-reactive isotopes can be used as indicators of particle mixing. Figure 5 shows the penetration of tracers into the sediments of control tubes 1 and 2 of L-302S, 16 d after spiking. A mixing rate of 3×10^{-7} to 4×10^{-7} cm$^2 \cdot$s^{-1} is needed to fit the profiles using the numerical transport model, which is also consistent with the observed removal rates from the water column (see section on removal mechanisms). Since no sediment profile could be obtained from the L-114 tubes after 16 d, our approach has to be more indirect. In 1982, 398 d after the spike, cores were taken from control tubes 1, 2, 19, and 20. Since 90% of the particle-reactive radiotracers (e.g. ^{113}Sn, ^{59}Fe, and ^{60}Co) were deposited to the sediments within 2 wk, we can treat the tracer deposition as having been instantaneous when interpreting the sediment distributions of the tracers in 1982. The sediment mixing coefficient D_B (square centimetres per second) can then be calculated from the following expression (Crank 1956):

$$(4) \quad C = C_0 \exp\left(-x^2/(4D_B \cdot \Delta t)\right)$$

where C = concentration of tracer in sediments (cpm per cubic centimetres), C_0 = concentration of tracer at the sediment–water interface (cpm per cubic centimetre), Δt = elapsed time (seconds), and x = depth (centimetres). In Fig. 6a and 6b, the normalized activities of particle-reactive ^{60}Co (= C/C_0) in the 1982 cores are plotted versus depth squared. From the slope and Δt, we can calculate $D_B = 2.5 \times 10^{-8}$ cm$^2 \cdot$s^{-1} for L-302S

TABLE 7. Radiotracer mass balance for control tubes L-302S and L-114 (decay corrected).

	Day	L-302S			L-114		
		^{113}Sn	^{60}Co	^{134}Cs	^{113}Sn	^{60}Co	^{134}Cs
Tube 1							
(1) Σ Water (%)[a]	87	5	1	13	0.5	2	7
(2) Σ Sediment (%)[b]	398	80	61	83	4	8.5	17
(3) Σ Walls (%)	18	5	5	5	5	5	5
(4) Σ Leakage (%)	87	25	25	25	30	30	30
(5) Sum 2–4 (%)	—	110	90	110	40	45	52
(6) Σ Sediment trap (%)[c]	17	51	53	2	89	88	5
Tube 2							
(1) Σ Water (%)[a]	87	—	20	20	—	47	12
(2) Σ Sediment (%)[b]	398	—	77	77	—	35	31
(3) Σ Walls (%)	18	—	5	5	—	5	5
(4) Σ Leakage (%)	87	—	13	13	—	20	20
(5) Sum 2–4 (%)		—	95	95	—	60	55
(6) Σ Sediment trap (%)[c]	17	—	42	1	—	83	2

[a] Fraction of isotope added remaining in the water column on day 87.

[b] Inventory of isotope in sediment on day 398 as fraction of amount added.

[c] Fraction of isotope added that could be accounted for by settling particles collected with sediment traps through day 17.

tubes 1 and 2 and 1×10^{-7} cm$^2 \cdot$s^{-1} for L-114 tubes 19 and 20. If we assume that the ratio of the rate of benthic mixing in the surface sediments of L-302S to the rate of mixing in L-114 remained constant during our experiment, then we calculate $D_B = 1.6 \times 10^{-6}$ cm$^2 \cdot$s^{-1} for L-114 sediments during the summer of 1981 by multiplying the 1981 mixing rate in L-302S tubes by the ratio of the long-term mixing rate in L-114 to the long-term mixing rate in L-302S. The long-term mixing rates derived from the 1982 sediment tracer profiles are lower limits for the summer time only, since sediment mixing is mostly a function of the benthic macrofauna activity, which would be high only during the warm summer months, i.e. at most, one third of a year. Also, there is probably less physical mixing of sediment for about 6 mo under winter ice-cover. This may explain why the mixing rate calculated for tubes 1 and 2 using results from day 16 is approximately an order of magnitude larger than the rate calculated using results from day 398. Furthermore, these benthic mixing rates are a function of depth (Kipphut 1978). It is therefore not straightforward to extrapolate from a long-term mixing rate measured over a depth interval of several centimetres to one that applies only in the upper 1–2 cm of surface sediments in the warm summer months, and we must work with a considerable uncertainty in D_B for L-114 tubes.

Mass Balance of Radiotracers in the Tubes

A mass balance is the foundation of any interpretation of a tracer experiment in a multicompartment system. Unfortunately in our experiments we could not monitor each reservoir on the same date. In Table 7, the mass balance for control tubes 1, 2, 19, and 20 is shown for sediments on day 398, for the water on day 87, and for sediment traps and walls on day 17 or 18. It is, however, still very useful for a number of reasons: (1) we can check for artifacts such as well adsorption or wall leakage, (2) we can compare the amounts caught in sediment traps with that expected from water column activities on that date, and (3) we can still rely on the mass balance for isotope tracers which are removed from the water column on time scales shorter than the shortest date.

It can be seen from Table 7 that the tubes neither adsorbed nor lost the tracers to any great extent: wall adsorption is a sink for ≤5% of the added tracers. If little tracer activity is found on the walls on day 18, when many tracers are already mostly in the sediments, then one can expect the same situation on day 87 or 398. Generally, the tubes did not leak by more than 30%, although higher percentages did occur occasionally as could be deduced from the rate of loss of ^{22}Na from the water column. We therefore normalized all tracer activities to those of ^{22}Na.

What is found in the water or in the sediments on day 87 should be similar to that on day 398, if little if left in the water on day 87. This was generally the case in L-302S.

Most of the tracer activity removed from the water of L-302S tubes is found in the sediments (Table 7). This was not the case in L-114 tubes 19 and 20, where only 30% or less of the added tracers is found in the sediments. This might be due to nonrepresentative sampling.

Effect of pH on Metal Removal

Figures 7–9 show the change in water column activities (expressed as the fraction of the initial activity) with time in selected tubes of both lakes for selected isotopes. After 18 d, the pH of most of the tubes was lowered to 4.8 by adding HCl, after which some of the isotopes started to diffuse back into the water column. After 37 d, the pH of some of the acidified tubes (1, 3, and 16) was raised to their initial values between 6.5 and 7.0 by adding $CaCO_3$. Removal of the acid-sensitive metals (Co, Mn, and Zn) resumed its preacidification pattern after the pH was raised by liming. In other tubes the pH was held constant at 4.8 after day 37 and the water column tracer activities of Co, Mn, and Zn remained high. Different mechanisms can immobilize trace metals in sediments: sorption onto organic debris or hydrous oxides of Mn, Fe, or Al or, under reducing conditions, sorption or coprecipitation with iron sulfides. The labile behavior of Co, Mn, and Zn would argue strongly in favor of a reversible surface adsorption mechanism.

Other radioisotopes such as ^{134}Cs, ^{59}Fe, and ^{113}Sn as well as ^{75}Se, ^{110m}Ag, and ^{203}Hg (not shown here, unpubl. data) were little affected by both acid and subsequent $CaCO_3$ additions

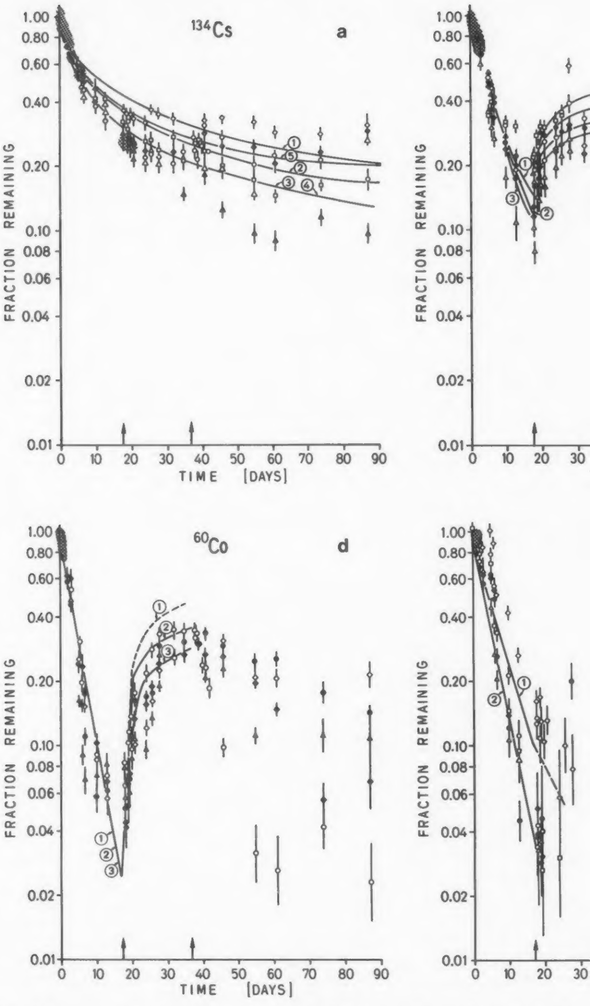
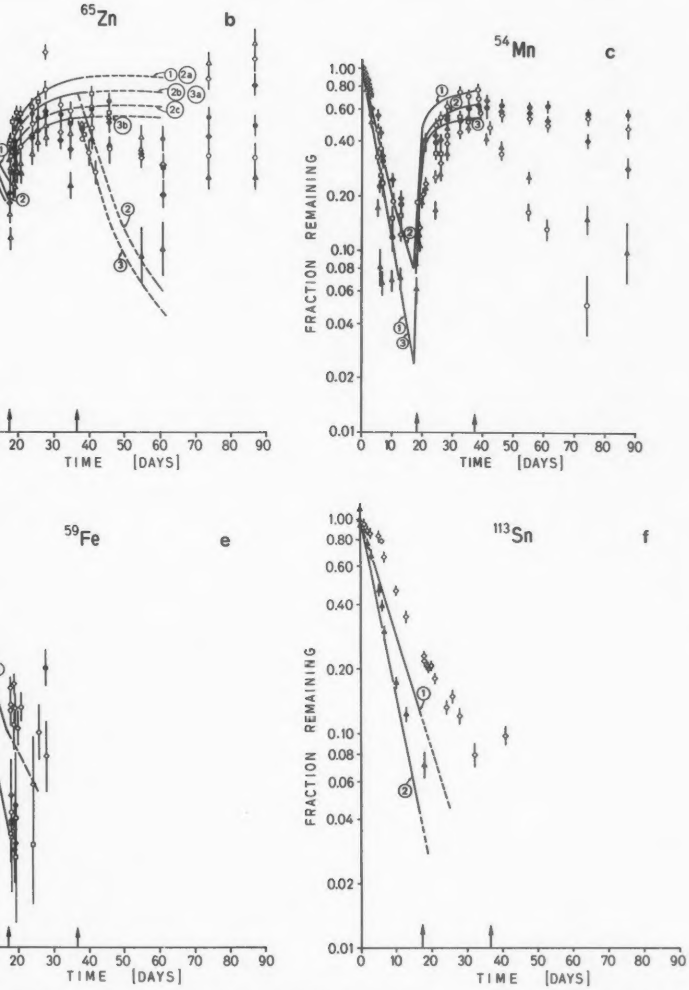


FIG. 7. Removal of radioisotopes as a function of the time of the experiment for L-114 tubes compensate for leakage (only ~ 5% of the ^{22}Na is removed to the sediments during the first deviation of the isotope ratio. The numbers on curves refer to model runs for which parameters maintained by the additions of HCl and $CaCO_3$, respectively. Curves 2 and 3 in Fig. 7b after 14; ○ = tube 16; △ = tube 18; □ = tube 20; ◆ = tube 15; ● = tube 17; ▲ = tube 19.



14 tubes 14−20. Day zero is 3 July 1981. Each isotope (*M) is normalized to the activity of ^{22}Na to
the first 60 d) and to the initial activity (i.e. $(^*M/^{22}Na) / (^*M_0/^{22}Na_0)$). Error bars indicate 1 standard
rameters are given in Table 8. The arrows on days 18 and 37 indicate the changes in pH conditions
7b after day 37 refer to a return to original pH conditions after addition of $CaCO_3$ to tube 16. ◇ = tube
be 19.

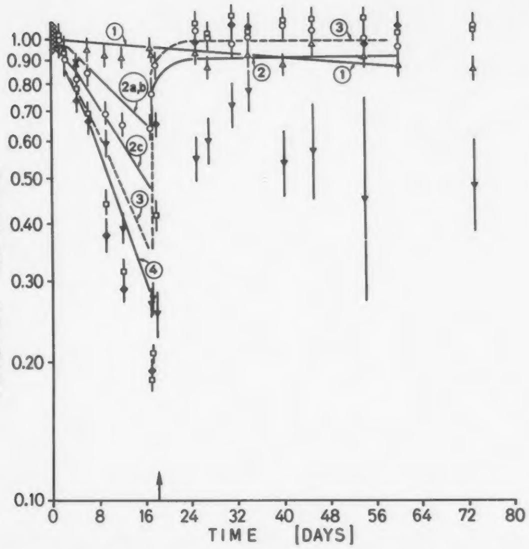


FIG. 8. Removal of radioisotopes from the water column of tube 13 as a function of time. Each isotope is normalized to ^{22}Na and to the initial activity ratio as in Fig. 7. Error bars indicate 1 standard deviation. The parameters of the model runs shown are given in Table 8. □ = ^{60}Co; ○ = ^{65}Zn; △ = ^{134}Cs; ◆ = ^{54}Mn; ▲ = ^{59}Fe.

(Fig. 7–9). While the acid-sensitive trace metals probably exist as cations, those trace metals not sensitive to pH could exist as colloids or as anions, or might have been sequestered by irreversible processes.

Sensitivity Analysis of the Transport Model

In principle, parameters measured by techniques outlined in Table 2 should determine the removal of the tracers. Under ideal conditions, one should be able to simulate the tracer removal using these measured parameters. However, not all parameters are known equally well. Measurements of each of the parameters often vary over a range of ±50% (z, F, V_p) or even a factor of 2 (D_B, K_D, k_1, and k_{-1}). Therefore, there is a range of parameter combinations which can fit the removal and back-diffusion data for the tracers, and a sensitivity analysis of the model is needed (Fig. 7–9). It was found, for example, that higher values of D_B can offset lower values of sorption rate constants $*k_1$ and k_{-1}. Also, a higher rate constant for removal (λ) or smaller rate constant for back-diffusion can be modelled by either increasing $*k_1$ in sediments or by increasing D_B throughout the experiment. Nevertheless, it is possible to use the numerical transport model to set upper and lower limits for each parameter which are in reasonable agreement with the other independently determined values. This is shown below.

Comparing model curves 2a and 3a in Fig. 9a illustrates the sensitivity of removal of the soluble tracer ^{134}Cs to the value of z. Model runs with z values of 0.1 and 0.2 cm bracket the observed removal, in agreement with z values derived from $CaSO_4$ plate dissolution (Table 6).

During the initial phase, adsorption to settling particles dominates removal of the most strongly adsorbed tracers (e.g. Fe, Sn, Co, and Mn), so removal of these tracers at neutral pH is insensitive to D_B as can be seen by comparing model runs 1 and 2 in Fig. 7c, and runs 1, 2, and 3 in Fig. 7d. However, removal of soluble tracers during the initial phase of the experiment (pH = 6.5–7.0) and back-diffusion of the acid-sensitive, particle-reactive metals (Co, Mn, and Zn) during the acidification phase (pH = 4.8) can both be used to check the consistency of the estimated sediment mixing rates (D_B). In L-302S tubes, removal of ^{134}Cs (Fig. 9a, curve 2b) and ^{65}Zn (Fig. 9b, curve 2) and back-diffusion of ^{65}Zn (Fig. 9b, curve 2), ^{54}Mn (Fig. 9C, curve 2), and ^{60}Co (Fig. 9, curve 2) are well reproduced using a model D_B of 0.8×10^{-7} cm$^2 \cdot$s^{-1}. This value is compatible with results obtained by modelling tracer distributions in cores collected on day 16 (Fig. 5), although the day 16 results permit a fairly wide range of D_B values. A substantially smaller value of D_B (2.5×10^{-8} cm$^2 \cdot$s^{-1}) was calculated from the penetration of tracers into the sediments of tubes 1 and 2 after 398 d (Fig. 6). However, as noted above, this is expected because sediment mixing during winter months is very much reduced.

Model runs for Cs, Zn, Mn, and Co in the L-114 tubes bracket the data using D_B values in the range of 53×10^{-7} to 116×10^{-7} cm$^2 \cdot$s^{-1}, substantially larger than the value of 16×10^{-7} cm$^2 \cdot$s^{-1} estimated by normalizing the results from the L-114 cores on day 398 to day 16 (see section on particle mixing). Therefore, either the assumptions involved in the normalization are in error, or very intense mixing of the upper 0–1 cm of sediments occurred in the L-114 tubes. Our tracer profiles in the sediments of tubes 19 and 20 on day 398 (Fig. 6a) do not have sufficient resolution to detect very intense mixing of the upper 0–1 cm. Such intense mixing is not unreasonable, however, because the high-porosity, flocculent surface sediments of L-114 are very easily mixed.

Other parameters were adjusted in the model runs to produce curves which fit the various data sets. For example, the kinetic constants for adsorption and desorption that provide reasonable model fits to the data in Fig. 7–9 are consistent with in situ $K_D(t)$ measurements using sediment trap and filtered material (compare AK_1/AK_2 in Table 8 with measured K_D values in Tables 3–5).

It was not our intention to bring the model fits to perfection but rather to show the sensitivity of the overall water column removal to each parameter. For future work we recommend the following strategy for the characterization of the transport parameters for tracer removal in lakes. Sorption kinetics on suspended particles have to be measured independently, and sediment traps should not be deployed in epilimnetic waters longer than 2 d. Incorporation of trace metals into particles can be rapid, e.g. it can take only hours to achieve equilibrium as in L-302S, or it can be slow as in L-114 where it took 1–5 d for the K_D values to approach a constant value. Whereas an equilibrium model would be adequate in L-302S, any model for L-114 must include the tracer uptake kinetics because some tracers do not achieve an adsorption–desorption equilibrium within the residence time of the particles in the water column. Therefore, models that incorporate adsorption kinetics are preferred for future work. Particle and radioisotope fluxes in the euphotic zone can be measured in sediment traps only during short exposure times of not more than 1–2 d in summer time.

Comparison with Radiotracer Studies in Whole Lakes or in Larger Enclosures

Our data strongly suggest that the variability of the tracer removal rates was caused by factors such as particle flux through the water column, particle mixing rates of surface sediments, and the turbulence-controlled thickness of the stag-

TABLE 8. Parameters for each model run.

					Phase					
Lake	Tube	Isotope	Run	Φ	AK$_1$ (cm^3·g^{-1}·d^{-1})	AK$_2$ (d^{-1})	K$_1$ (cm^3·g^{-1}·d^{-1})	K$_2$ (d^{-1})	K$_3$ (d^{-1})	*P* (g·cm^{-1})
302S	13	^{134}Cs	1	—	5×10^{3}	1	5×10^{3}	1	0	3×10^{-6}
		^{65}Zn	2a	—	2×10^{4}	0.5	2×10^{4}	0.5	0	3×10^{-6}
	(Fig. 8)	^{65}Zn	2b	—	9×10^{4}	1	9×10^{4}	1	0	4×10^{-6}
		^{65}Zn	2c	—	8×10^{4}	1	8×10^{4}	1	0	3×10^{-6}
		^{60}Co, ^{54}Mn	3	—	7.5×10^{4}	0.5	7.5×10^{4}	0.5	0	3×10^{-6}
		^{60}Co, ^{54}Mn	4a	—	8×10^{4}	0.4	8×10^{4}	0.4	0	3×10^{-6}
		^{59}Fe, ^{113}Sn	4b	—	1×10^{6}	1	1×10^{6}	1	0	4×10^{-6}
302S	1−3	^{134}Cs	1	0.7	2×10^{4}	2	1×10^{4}	2	0	2.3×10^{-6}
	(Fig. 9a)	^{134}Cs	2a	0.7	2×10^{4}	2	1×10^{4}	2	0	2.3×10^{-6}
			2b	0.7	2×10^{4}	2	1×10^{4}	2	0	2.3×10^{-6}
		^{134}Cs	3a	0.7	2×10^{4}	2	1×10^{4}	2	0	2.3×10^{-6}
			3b	0.7	2×10^{4}	2	1×10^{4}	2	0	2.3×10^{-6}
302S	1−3	^{65}Zn	1	0.7	2.5×10^{4}	1	2.5×10^{4}	1	0	3×10^{-6}
	(Fig. 9b)	^{65}Zn	2	0.7	8×10^{4}	1	6×10^{3}	1	0	2×10^{-6}
		^{65}Zn	3	0.7	2.5×10^{4}	1	2.5×10^{4}	1	0	3×10^{-6}
		^{65}Zn	4	0.7	8×10^{4}	1	8×10^{4}	1	0	3×10^{-6}
302S	1−3	^{54}Mn	1	0.7	3×10^{5}	1	7×10^{4}	1	0	2×10^{-6}
	(Fig. 9c)	^{54}Mn	2	0.7	3×10^{5}	1	7×10^{4}	1	0	2×10^{-6}
		^{54}Mn	3	0.7	1×10^{6}	1	1×10^{6}	1	0	2.3×10^{-6}
302S	1−3	^{60}Co	1	0.7	5×10^{4}	0.1	5×10^{4}	0.1	0	2×10^{-6}
	(Fig. 9d)	^{60}Co	2	0.7	1.5×10^{6}	1	2×10^{6}	1	0	2.3×10^{-6}
302S	1−3	^{59}Fe	1	0.7	3×10^{5}	1	5×10^{4}	1	0	2×10^{-6}
	(Fig. 9e)	^{59}Fe	2	0.7	1×10^{6}	1	1×10^{6}	1	0	2.3×10^{-6}
302S	1−3	^{113}Sn	1	0.7	3×10^{5}	1	5×10^{4}	1	0	2×10^{-6}
	(Fig. 9f)		2	0.7	1×10^{6}	1	1×10^{6}	1	0	2.3×10^{-6}
114	14−20	^{134}Cs	1	0.98	1×10^{4}	2	1×10^{4}	2	0	5×10^{-6}
		^{134}Cs	2	0.98	1×10^{4}	2	1×10^{4}	2	0	5×10^{-6}
	(Fig. 7a)	^{134}Cs	3	0.98	2.0×10^{4}	2	2.0×10^{4}	2	0	5×10^{-6}
		^{134}Cs	4	0.98	1.5×10^{4}	2	1.5×10^{4}	2	0	5×10^{-6}
		^{134}Cs	5	0.98	2×10^{4}	2	2×10^{4}	2	0	5×10^{-6}
114	14−20	^{65}Zn	1	0.98	7×10^{4}	1	7×10^{4}	1	0	5×10^{-6}
	(Fig. 7b)	^{65}Zn	2a	0.98	7×10^{4}	1	7×10^{4}	1	0	5×10^{-6}
		^{65}Zn	2b	0.98	7×10^{4}	1	7×10^{4}	1	0	5×10^{-6}
		^{65}Zn	2c	0.98	3.75×10^{4}	0.5	3.75×10^{4}	0.5	0	5×10^{-5}
		^{65}Zn	3a	0.98	7×10^{4}	1	7×10^{4}	1	0	5×10^{-6}
		^{65}Zn	3b	0.98	7×10^{4}	1	7×10^{4}	1	0	5×10^{-6}
114	14−20	^{54}Mn	1	0.98	7.5×10^{5}	0.5	7.5×10^{5}	0.5	0	5×10^{-6}
	(Fig. 7c)	^{54}Mn	2	0.98	7.5×10^{5}	0.5	7.5×10^{5}	0.5	0	5×10^{-6}
		^{54}Mn	3	0.98	7.5×10^{5}	0.5	7.5×10^{5}	0.5	0	5×10^{-6}
114	14−20	^{60}Co	1	0.98	4.5×10^{5}	0.3	4.5×10^{5}	0.3	0	5×10^{-6}
	(Fig. 7d)	^{60}Co	2	0.98	4.5×10^{5}	0.3	4.5×10^{5}	0.3	0	5×10^{-6}
		^{60}Co	3	0.98	4.5×10^{5}	0.3	4.5×10^{5}	0.3	0	5×10^{-6}
114	14−20	^{59}Fe	1	0.98	1.5×10^{4}	0.1	1.5×10^{4}	0.1	0	4×10^{-6}
	(Fig. 7e)	^{59}Fe	2	0.98	1×10^{6}	1	1×10^{6}	1	0	5×10^{-6}
114	14−20	^{113}Sn	1	0.98	1.5×10^{4}	0.1	1.5×10^{4}	0.1	0	4×10^{-6}
	(Fig. 7f)	^{113}Sn	2	0.98	1.5×10^{6}	1	1.5×10^{6}	0.1	0	5×10^{-6}

	Phase 1						Phase 2			
n^{-1})	F ($g \cdot cm^{-2} \cdot d^{-1}$)	V_p ($cm \cdot d^{-1}$)	R ($g \cdot cm^{-2} \cdot d^{-1}$)	D_B (10^{-7} $cm^2 \cdot s^{-1}$)	D_m (10^{-6} $cm^2 \cdot s^{-1}$)	z (cm)	AK_1 ($cm^3 \cdot g^{-1} \cdot d^{-1}$)	AK_2 (d^{-1})	K_1 ($cm^3 \cdot g^{-1} \cdot d^{-1}$)	K_2 (d^{-1})
10^{-6}	1×10^{-4}	30	0	0	0	0.06	5×10^3	1	5×10^3	1
10^{-6}	1×10^{-4}	30	0	0	0	0.06	1.3×10^3	1	$1.\times10^3$	1
10^{-6}	5×10^{-5}	12.5	0	0	0	0.06	1.3×10^3	1	1.3×10^3	1
10^{-6}	1×10^{-4}	30	0	0	0	0.06	—	—	—	—
10^{-6}	1×10^{-4}	30	0	0	0	0.06	2.3×10^3	1	2.3×10^3	1
10^{-6}	1×10^{-4}	30	0	0	0	0.06	—	—	—	—
10^{-6}	5×10^{-5}	12.5	0	0	0	0.06	5×10^3	—	5×10^3	1
10^{-6}	7×10^{-5}	30	0	0	19.5	0.1	2×10^4	2	1×10^4	2
10^{-6}	7×10^{-5}	30	0.01	0.08	19.5	0.2	2×10^4	2	2.8×10^3	2
10^{-6}	7×10^{-5}	30	0.10	0.80	19.5	0.2	2×10^4	2	2.8×10^3	2
10^{-6}	7×10^{-5}	30	0.01	0.08	19.5	0.1	2×10^4	2	2.8×10^3	2
10^{-6}	7×10^{-5}	30	0.01	0.08	19.5	0.1	2×10^4	2	1×10^4	2
10^{-6}	1×10^{-4}	35	0.06	0.5	7	0.05	1.3×10^2	1	1.3×10^2	1
10^{-6}	1×10^{-4}	50	0.1	0.8	7	0.06	1.3×10^3	1	2.3×10^2	1
10^{-6}	1×10^{-4}	35	0.6	4.8	7	0.05	1.3×10^2	1	1.3×10^2	1
10^{-6}	1×10^{-4}	35	0.01	0.08	7	0.05	2×10^2	1	2×10^2	1
10^{-6}	1×10^{-4}	50	0.1	0.8	6	0.06	8×10^2	1	2.3×10^2	1
10^{-6}	1×10^{-4}	50	0.1	0.8	6	0.06	8×10^2	1	8×10^2	1
10^{-6}	7×10^{-5}	30	0.1	0.8	6	0.06	8×10^2	1	8×10^2	1
10^{-6}	1×10^{-4}	50	0.35	2.8	6	0.06	1.4×10^3	1	1.4×10^3	1
10^{-6}	7×10^{-5}	30	0.1	0.8	6	0.06	9×10^2	1	9×10^2	1
10^{-6}	1×10^{-4}	50	0.1	0.8	2	0.06	1×10^5	1	7×10^3	1
10^{-6}	7×10^{-5}	30	0.1	0.8	2	0.06	—	—	—	—
10^{-6}	1×10^{-4}	50	0.1	0.8	2	0.06	3×10^5	1	8×10^4	1
10^{-6}	7×10^{-5}	30	0.1	0.8	2	0.06	—	—	—	—
10^{-6}	1.4×10^{-4}	30	0.46	53	19.5	0.05	—	—	—	—
10^{-6}	1.4×10^{-4}	30	1.0	116	19.5	0.05	—	—	—	—
10^{-6}	1.4×10^{-4}	30	0.46	53	19.5	0.05	—	—	—	—
10^{-6}	1.4×10^{-4}	30	1.0	116	19.5	0.05	—	—	—	—
10^{-6}	1.4×10^{-4}	30	0.14	16	19.5	0.05	—	—	—	—
10^{-6}	1.4×10^{-4}	30	0.14	16	7	0.03	4×10^3	1	4×10^3	1
10^{-6}	1.4×10^{-4}	30	0.46	53	7	0.03	2×10^3	1	2×10^3	1
10^{-6}	1.4×10^{-4}	30	0.46	43	7	0.03	4×10^3	1	4×10^3	1
10^{-5}	1.4×10^{-4}	30	0.46	53	7	0.03	5×10^3	1	5×10^3	1
10^{-6}	1.4×10^{-4}	30	1.0	116	7	0.03	2×10^3	1	2×10^3	1
10^{-6}	1.4×10^{-4}	30	1.0	116	7	0.03	4×10^3	1	4×10^3	1
10^{-6}	1.4×10^{-4}	30	0.46	53	6	0.03	2.3×10^2	1	2.3×10^2	1
10^{-6}	1.4×10^{-4}	30	0.14	16	6	0.03	1×10^3	1	1×10^3	1
10^{-6}	1.4×10^{-4}	30	0.46	53	6	0.03	1×10^3	1	1×10^3	1
10^{-6}	1.4×10^{-4}	30	0.14	16	6	0.03	4×10^3	1	4×10^3	1
10^{-6}	1.4×10^{-4}	30	0.46	53	6	0.03	4×10^3	1	4×10^3	1
10^{-6}	1.4×10^{-4}	30	1.0	116	6	0.03	4×10^3	1	4×10^3	1
10^{-6}	1.5×10^{-4}	40	0.1	6	2	0.03	7×10^4	1	7×10^4	1
10^{-6}	1.4×10^{-4}	30	0.1	6	2	0.03	1.5×10^5	1	1.5×10^5	1
10^{-6}	1.5×10^{-4}	40	0.1	6	2	0.03	2×10^5	1	4×10^5	1
10^{-6}	1.4×10^{-4}	30	0.1	6	2	0.03	—	—	—	—

TABLE 8. (*Concluded*)

Lake	Fig.	Isotope	Run	Φ	K$_1$ (10^4 cm$^3 \cdot$ g$^{-1} \cdot$ d^{-1})	K$_2$ (d^{-1})	K$_3$ (d^{-1})	*P* (10^{-6} g$\cdot$ cm^{-3})	*F* (10^{-5} g$\cdot$ cm$^{-2} \cdot$ d^{-1})
223	Fig. 11a	^{134}Cs	1	0.7	1	2	0	4	10
		^{134}Cs	2	0.7	1	2	0	4	10
		^{134}Cs	3	0.7	1	2	0	4	10
	Fig. 10	^{60}Co	1	0.7	100	1	0	4.7	14
		^{60}Co	2	0.7	220	1	0	2.3	7
224	Fig. 11b	^{134}Cs	1	0.7	1	2	0	4	10
		^{134}Cs	2	0.7	1	2	0	3	10
	Fig. 10	^{60}Co	1	0.7	100	1	0	4.7	14
		^{60}Co	2	0.7	220	1	0	2.3	7
226NE	Fig. 11c	^{134}Cs	1	0.7	1	2	0	4	10
226SW		^{134}Cs	2	0.7	1	2	0	4	10
226NE	Fig. 10	^{60}Co	1	0.7	100	1	0	4.7	14
		^{60}Co	2	0.7	220	1	0	2.3	7
226SW	Fig. 10	^{60}Co	1	0.7	100	1	0	4.7	14
		^{60}Co	2	0.7	220	1	0	2.3	7

NOTE: Phase 1 or 2 = 0−18 or 18−37 d of experiment. During phase 2, only the *K* and AK values c
constant for adsorption on suspended particles ($*k_1$); AK$_2$ = rate constant for desorption from suspe
in sediments (k_{-1}); K_3 = rate constant for lattice position transport or oxidation; *P* = concentration of su
this particle mixing rate constant = $D_B\ (1 - \Phi)\rho/\Delta z$; D_B = benthic particle mixing rate (variable); D_m
sublayer thickness; λ_1 = removal rate constant for ^{60}Co in tubes 1 and 2, L-302S; λ_2 = removal rate
for depth increase; λ_{dil_1}, λ_{dil_2} = dilution rate constant as correction for epilimnion deepening; Δt = tim
of exposed sediments, *V* = volume of epilimnion.

F (10^{-5} g· $^{-2}$·d^{-1})	V_p (cm· d^{-1})	R (g·cm^{-2}· d^{-1})	D_B (10^{-7} cm^2·s^{-1})	D_m (10^{-6} cm^2·s^{-1})	z (cm)	λ_{dil_1} (d^{-1})	Δt (d)	λ_{dil_2} (d^{-1})	λ (d^{-1})	h_0 (cm)	a (d^{-1})
10	50	4.6	37	19.5	0.08	—	—	—	—	—	—
10	30	0.1	0.8	19.5	0.05	—	—	—	—		
10	30	0.1	0.8	19.5	0.10	—	—	—	—		
14	25	0.5	4	6	0.06	—	—	—	0.094	220	0
7	30	0.5	4	6	0.06	—	—	—	0.114	220	0
10	25	4.6	37	19.5	0.05	0.05	5	0.007	—	—	—
10	30	0.6	4.8	19.5	0.05	0.05	9	0.007	—		
14	25	0.5	4	6	0.06	—	—	—	0.035	600	7.9×10^{-3}
7	30	0.5	4	6	0.06	—	—	—	0.042	600	7.9×10^{-3}
10	30	4.6	37	19.5	0.05	0.007	60		—		
10	30	4.6	37	19.5	0.05	*AV*	60		—		
14	25	0.5	4	6	0.06	—	—	—	0.069	300	1.25×10^{-2}
7	30	0.5	4	6	0.06	—	—		0.083	300	1.25×10^{-2}
14	25	0.5	4	6	0.06	—	—	—	0.069	300	9.5×10^{-3}
7	30	0.5	4	6	0.06	—	—	—	0.083	300	9.5×10^{-3}

K values change. All other parameters remain constant from phase 1. Parameters: Φ = porosity in sediments; AK$_1$ rate
om suspended particles (k_{-1}); K_1 = rate constant for adsorption in sediments ($^*k_1$); K_2 = rate constant for desorption
tion of suspended particles F = particle flux; V_p = settling velocity of particles; ρ = dry density of sediments; R = ben-
iable); D_m = molecular diffusion coefficient (taken from Li and Gregory 1974); z = stagnant film thickness = diffusive
oval rate constant for ^{60}Co in tubes 19 and 20, L-114; $h = h_0\,(1 + at)$ = epilimnion depth, $h_0 = h$ at $t = 0$; a = factor
Δt = time of change from λ_{dil_1} to λ_{dil_2}; $AV = A(t)$ and $V(t)$ taken from hydrographic and temperature data, A = area

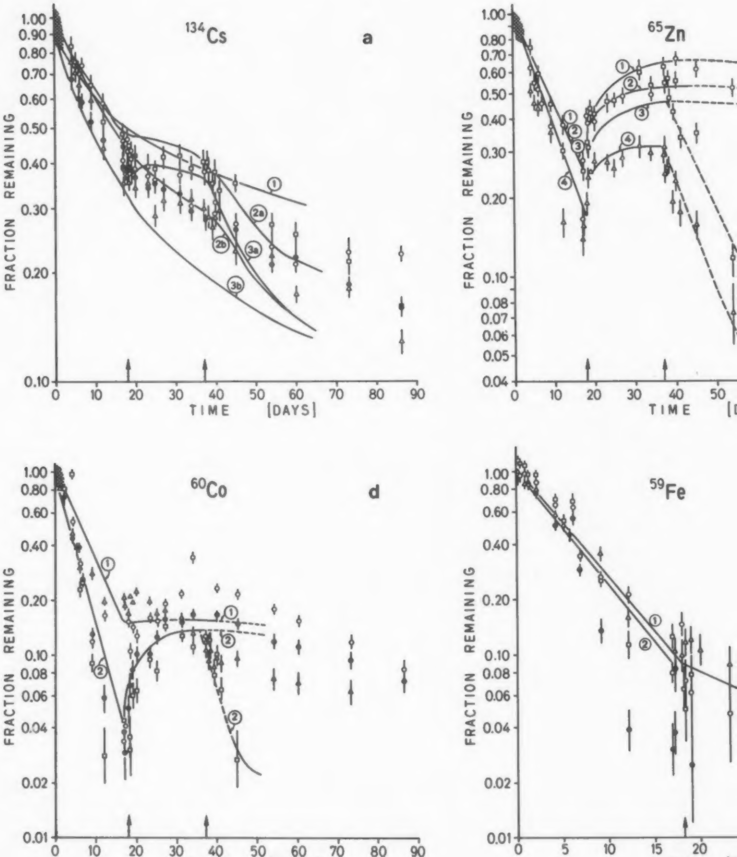
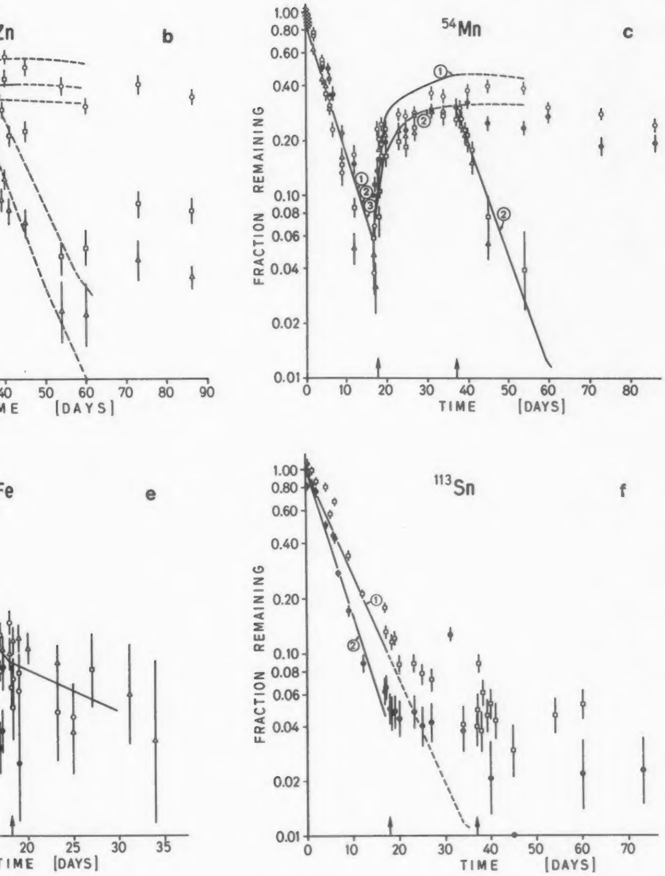


FIG. 9. Removal of radioisotopes as a function of time for L-302S tubes 1, 2, 3, and 8. The activity
The parameters of the model runs shown are given in Table 8. The pH was reduced to 4.8 by additio
curve 1 in Fig. 9d represent a return to original pH conditions for the tubes that received $CaCO_3$ (i.e. tu



activity of each istotope is normalized as in Fig. 7, and error bars indicate 1 standard deviation. addition of HCl on day 18. After day 37, curves 3 and 4 in Fig. 9b, curve 2 in Fig. 9c, and (i.e. tubes 1 and 3). □ = tube 1; ○ = tube 2; △ = tube 3; ● = tube 8.

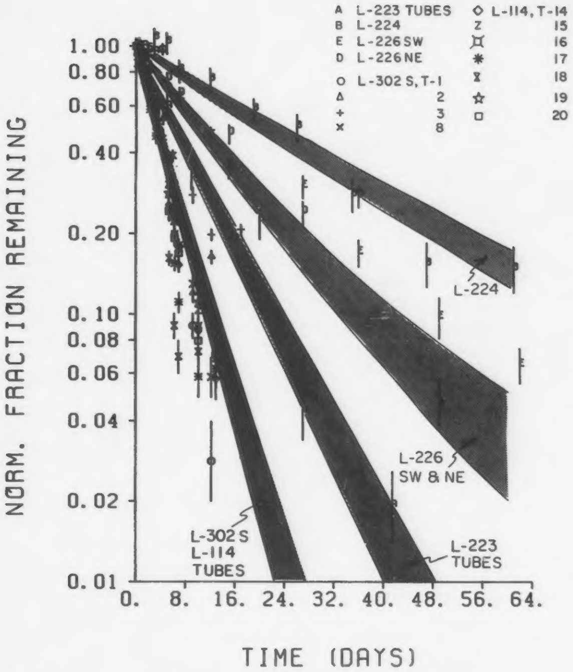


FIG. 10. Measured removal rates of ^{60}Co in tubes in L-114, L-302S, and L-223 (Schindler et al. 1980) and in whole lakes L-224 (Hesslein et al. 1980) and L-226 (NE and SW basins together, R. H. Hesslein, unpubl. data) compared with removal rates predicted using particle fluxes and settling velocities observed in L-114 and L-302S tubes. The parameters used are given in Table 8. The shaded areas represent the possible range in the removal curve for each lake given the uncertainty in the transport parameters.

nant boundary film overlying the sediments. Chemical processes that control the sorption onto uptake by particles are, however, quite similar in the two different lakes. We will therefore use the average values of these physical particle or solution parameters and apply them to the whole-lake radiotracer experiments.

Two key isotopes, ^{60}Co for transport on setting particles and ^{134}Cs for direct sediment uptake, can be used to test whether the set of parameters derived from the small tubes is applicable to larger bodies of water. These isotopes were added to larger enclosures in L-223 and to two whole lakes (L-224 and L-226) in earlier experiments (Schindler et al. 1980; Hesslein et al. 1980; R. H. Hesslein, unpubl. data). The epilimnion deepened from about 5 to 7 m during the L-224 experiment and from 3 to 7 m during the portion of the L-226 experiment for which we are using the results (D. W. Schindler, unpubl. ELA data reports). Epilimnion deepening not only diluted the concentration of the tracers by increasing the volume of the epilimnion, but it also changed the removal rate constant for particle-reactive tracers such as ^{60}Co by increasing the depth a tagged particle had to fall in order to be removed from the mixed layer. This can be taken into account by increasing the measured depth of the thermocline in the first-order removal term, i.e.

$$(5)\quad \lambda_s(t) = \frac{V_p \cdot f_p}{h(t)}$$

where $h(t) = h_o\,(1 + a \cdot t)$ = mean epilimnion depth determined from temperature profiles, V_p = settling velocity, f_p = fraction on particles, t = time, and a = a constant determined empirically. The removal of ^{60}Co in L-223, L-224, L-226, and in the tubes of L-114 and L-302S is plotted in Fig. 10. While we were able to determine our individual parameters rather well in the small tubes, the scatter of the whole-lake data would preclude an equally precise determination of the parameters from these results. The model runs in Fig. 10 are calculated using equation 5, measured values of $h(t)$, and average values derived from our L-302S and L-114 tube experiments for V_p, C_p, $*k_1$, k_{-1}, and f_p. They fit the data rather well. Our average value of V_p = 30 cm·d^{-1} for both L-302S and L-114 tubes agrees with values which can be calculated from ^{60}Co removal rates in the earlier radiotracer experiments; i.e. for L-224 (recalculated from Hesslein et al. 1980 = using (see equation 5): $V_p = h \cdot \lambda_{\mathrm{Co\text{-}60}}/f_p = 700\ \mathrm{cm} \cdot 0.036 \cdot \mathrm{d}^{-1}/0.85 = 30\ \mathrm{cm} \cdot \mathrm{d}^{-1}$; for L-223 control tube D: $V_p = 220\ \mathrm{cm} \cdot 0.10 \cdot \mathrm{d}^{-1}/0.97 = 23\ \mathrm{cm} \cdot \mathrm{d}^{-1}$; and for control tube E: $V_p = 220\ \mathrm{cm} \cdot 0.105 \cdot \mathrm{d}^{-1}/0.88 = 26\ \mathrm{cm} \cdot \mathrm{d}^{-1}$ (calculated from Schindler et al. 1980).

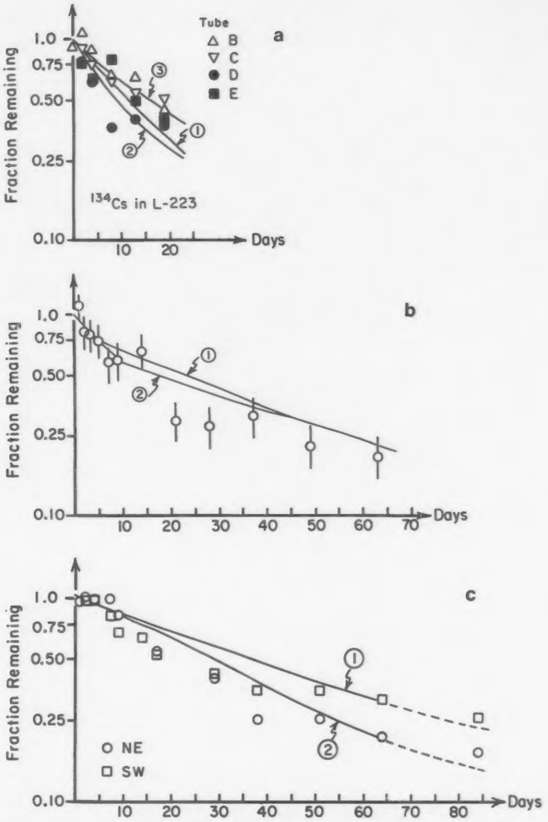


FIG. 11. Removal curves of ^{134}Cs from the epilimnetic water column for (a) enclosures in L-223 (Schindler et al. 1980), (b) L-224 (Hesslein et al. 1980), and (c) L-226 (R. H. Hesslein, unpubl. data). Model curves, whose parameters are given in Table 8, are shown for comparison.

Apparent removal rates of more soluble radiotracers such as ^{134}Cs are affected even more than the particle-reactive metals by the epilimnion deepening dilution mechanism, since they have a longer residence time in the water column. In the model

TABLE 9. Comparison of initial first-order removal rate constants λ_i^0 (d^{-1}) observed in whole-lake experiments with those predicted λ_i^p from the limnocorral experiments.[a]

Isotope	K_D ($cm^3 \cdot g^{-1}$)	L-224 λ_i^p	L-224 λ_i^0	L-226 λ_i^p	L-226 λ_i^0
^{60}Co	1.5×10^6	0.08	0.05	0.08	0.06
^{59}Fe	1×10^6	0.08	0.04	0.07	0.07
^{65}Zn	1×10^5	0.06	0.03	0.04	0.05
^{203}Hg	3×10^5	0.08	0.06	0.07	0.07
^{75}Se	5×10^4	0.06	0.05		
^{134}Cs	7.5×10^3	0.06	0.06	0.03	0.05

	h (m)	V/A (m)	λ_{dil} (d^{-1})	V_p ($cm \cdot d^{-1}$)	C_p ($mg \cdot L^{-1}$)
L-224	6	17	0.05	30	4
L-226S,N	3	10	0.007	30	4

NOTE: z was assumed to be 0.1 cm for ^{134}Cs and 0.05 cm for all the other isotopes.

[a] Assuming $\lambda_{ip} = \lambda_s + \lambda_{SWI} + \lambda_{dil}$ where

$$\lambda_s = \frac{V_p \cdot f_p}{h}; \lambda_{SWI} = \frac{D \cdot A}{z \cdot V}(1 - f_p).$$

curves in Fig. 11a−11c, we have included this in the model as either a simple dilution correction or, more accurately, as an increase in total epilimnion volume and sediment surface area available for direct uptake of the tracer (model run 2, Fig. 11c). Epilimnion volume and the area of exposed surface sediments were calculated for each thermocline depth using available morphometric data for the lakes (Hesslein et al. 1980; D. W. Schindler, unpubl. ELA data reports). By using parameters derived from our tube experiments (Table 8), model curves consistent with ^{134}Cs removal in larger tubes and in whole lakes can be attained (Fig. 11a−11c). The long-term concentration of the more soluble tracers such as ^{134}Cs in the lake water will be controlled by the tracer K_D in the sediments and the depth of sediment mixing, both of which would have to be determined more accurately in order to predict the steady-state concentration of ^{134}Cs in L-224 or L-226. We conclude, therefore, that the removal behavior of other isotopes used in the whole-lake experiments will be controlled by the same mechanisms as these two key isotopes, ^{60}Co and ^{134}Cs. Their initial removal rates can also be predicted quite well when using the results from our limnocorral experiments and our simple removal model (Table 9).

Implications of the Results to the Acidification of Lakes by Acid Rain

Earlier studies in limnocorrals of the effects of acidification on radiotracer removal pathways in ELA lakes (Schindler et al. 1980) showed that decreasing the fraction of the total radiotracer concentration that is absorbed to suspended particles (f_p) by lowering the pH from 7.0 to 5.1 did not change the initial removal rates by very much. This can be explained by our results which indicate that the transfer coefficients for both removal pathways (i.e. adsorption of particle reactive metals to settling particles and adsorption of soluble tracers by surface sediments) are of similar magnitude, i.e. $V_p \cong 30\ cm \cdot d^{-1}$, $D_m/z \cong 9 - 34\ cm \cdot d^{-1}$. The overall initial removal rate constant (λ_i) obtained by combining equations 1 and 3 is

$$(6) \quad \lambda_i = V_p \cdot f_p / h + \frac{D_m \cdot A}{z \cdot V}(1 - f_p)$$

which, in enclosures, reduces to $\lambda_i \cong V_p/h$, since $V/A = h$ and $V_p \cong D_m/z$. Therefore, λ_i is independent of f_p, and any acid-induced change in f_p does not seriously affect λ_i when the tracer is added after the acid. However, due to the lower K_D for many metals at lower pH, the higher steady-state concentrations of metals in solution at pH = 5.1 compared with pH = 7.0 observed by Schindler et al. (1980) would still be expected.

Many areas affected by acid rain also receive higher loadings of trace metals (e.g. Jeffreys and Snyder 1981). Increased lake water concentrations of trace metals can be due to mobilization from sediments, mobilization from watershed soils, or increased inputs from direct atmospheric deposition. We have carried out trace metal additions as part of these experiments which provide some indication on how increased metal loadings affect trace metal behavior. Stable Fe, Mn, and Zn were added to tubes 14, 15, and 16, respectively (Table 1). No effect on in situ K_D or on λ_i for ^{54}Mn, or ^{65}Zn was observed in any of these tubes (Fig. 7b and 7c). In contrast, K_D of ^{59}Fe in tube 14, which received an addition of stable Fe, was smaller than in other tubes. This measurably slowed the removal of ^{59}Fe from the water column of tube 14 compared with that in the other tubes (Fig. 7d), possibly because the increased Fe loading saturated the adsorption capacity of the particles. Also, the combined addition of trace metals and acid would slow down the removal of these elements from the water column.

Additions of $CaCO_3$ to acidified tubes to simulate the effect of liming an acidified lake restored the initial removal conditions for the acid-sensitive metals (e.g. compare the results after day 37 for Zn, Mn, and Co in tube 1, which received $CaCO_3$, with tube 2, which did not, in Fig. 9b−9d). Higher nutrient supplies to tubes 3 and 18, which caused slightly higher particle fluxes and pH due to eutrophication, did not have dramatic effects on trace metal removal behavior in these shallow systems. Addition of $CaCO_3$ to tube 3 after acidification restored the higher than normal primary productivity. One important difference between tube 3 and the other tubes could be observed: additions of both HCl and $CaCO_3$ to tube 3 did not affect the removal behavior of ^{60}Co (and ^{57}Co, not shown) by very much. ^{60}Co (and ^{57}Co, not shown) continued to be removed after acid additions, but was removed more slowly after $CaCO_3$ addition than expected from its behavior in control tube 1. We do not yet have a good explanation for this unusual behavior of Co, but our results are in agreement with the whole-lake studies of R. H. Hesslein (unpubl. data) who found no significant difference in trace metal removal rates in L-226N (eutrophied by adding phosphate) and L-226S, except for Co, which was less rapidly removed from the eutrophied basin.

Our tube experiments indicate, therefore, that the radiotracer pathways are controlled initially as much by physical processes of particle settling in the water column, particle mixing in the surface sediments, and the thickness of the turbulence-related "equivalent boundary film" as they are by chemical processes. In conclusion, it is found that the two approaches of radiotracer experiments, in enclosures or in whole lakes, complement each other nicely by allowing the more accurate determination of transport parameters for trace element removal on shorter time scales in small enclosures but giving better insights into the long-term cycling of radioactive trace metals in whole-lake experiments.

Acknowledgments

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Fundy Tidal Power Development and Potential Fish Production in the Gulf of Maine[1]

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Campbell, D. E., and J. S. Wroblewski. 1986. Fundy tidal power development and fish production in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 43: 78–89.

The possible effects of tidal amplitudes altered by Fundy tidal power development upon potential fish production in the Gulf of Maine are examined with a marine ecosystem model. Three areas off the Maine coast are delineated on the basis of winds, tides, and the extent of vertical mixing. An optimum kinetic energy from wind and tide exists for maximum primary production in the water column. Primary production in the model is the base for a simple pelagic food chain leading from phytoplankton through zooplankton to fish. If the construction of a tidal power dam in the upper Bay of Fundy results in a 5–10% increase in tidal amplitude, our first-order model predicts that enhanced vertical mixing from May to October will increase potential fish production along the Maine west coast by 7–12%. Fish production along the Maine east coast and in offshore waters is predicted to remain at present levels. Climatic variation is predicted to have as large an impact on fish production as man-induced changes in vertical mixing caused by tidal power development.

Les auteurs utilisent un modèle d'écosystème marin pour étudier les effets éventuels de la modification de l'amplitude des marées, causée par l'usine marémotrice de la baie de Fundy, sur la production piscicole dans le golfe du Maine. Trois zones au large des côtes du Maine sont délimitées en fonction des vents, des marées et de l'importance du mélange vertical. Il existe une énergie cinétique optimale due aux vents et aux marées permettant une production primaire maximale dans la colonne d'eau. Dans le modèle, la production primaire sert de base à une chaîne alimentaire pélagique simple phytoplancton – zooplancton – poisson. Le modèle d'ordre premier prévoit, suite à la construction d'un barrage marémoteur dans la partie d'amont de la baie qui provoquera une augmentation de 5 à 10 % de l'amplitude des marées, que l'accroissement du mélange vertical de mai à octobre pourrait se traduire par une augmentation de 7 à 12 % de la production de poissons le long de la côte ouest du Maine. La production le long de la côte est, et celle des eaux du large, devraient demeurer constantes. On prévoit que les effets des variations climatiques sur la production de poissons seront aussi importants que ceux des modifications du mélange vertical découlant de la construction de l'usine marémotrice.

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If the Fundy Tidal Power Corporation constructs a dam across the Minas Basin in the Bay of Fundy, there may be a change in the tidal range in the Gulf of Maine. A hydrodynamic, mathematical model of the Gulf of Maine – Bay of Fundy system developed by Greenberg (1979) predicts that tidal height along the Maine coast may be increased by 10% if such a dam is built. In general, a 10% change in tidal current speed would be expected to accompany the amplitude change along the Maine coast. Garrett (1984) estimated that there will be an average change of 5% in tidal velocities averaged over the entire Gulf. He points out that this velocity change in turn gives approximately a 15% change in the energy available for vertical mixing because the energy transferred to vertical mixing is proportional to the cube of the tidal velocity.

Intuitively one might expect that tidal amplitudes would be decreased by the construction of a dam, due to the damping effect of water containment for electric power generation. However, Garrett (1972) showed by means of frequency response analysis that the Gulf of Maine and the Bay of Fundy behave as a single system with a resonant period of about 13.3 h. This natural period of oscillation for the system is close to 12.4 h which is the period of the M_2 tidal component. If the length of this system were to be shortened by building a dam, the natural frequency of oscillation of the basin would move closer to its forcing frequency (i.e. the system would be closer to resonance) and therefore, the tidal amplitude would increase. For practical purposes this change in tidal amplitude represents a permanent shift in the energy available for vertical mixing in the Gulf of Maine ecosystem.

This change in vertical mixing may have important ecological effects. To determine whether or not the proposed dam is in the best interest of society, the environmental as well as economic impacts of the development of Fundy tidal power must be evaluated. The energy circuit language developed

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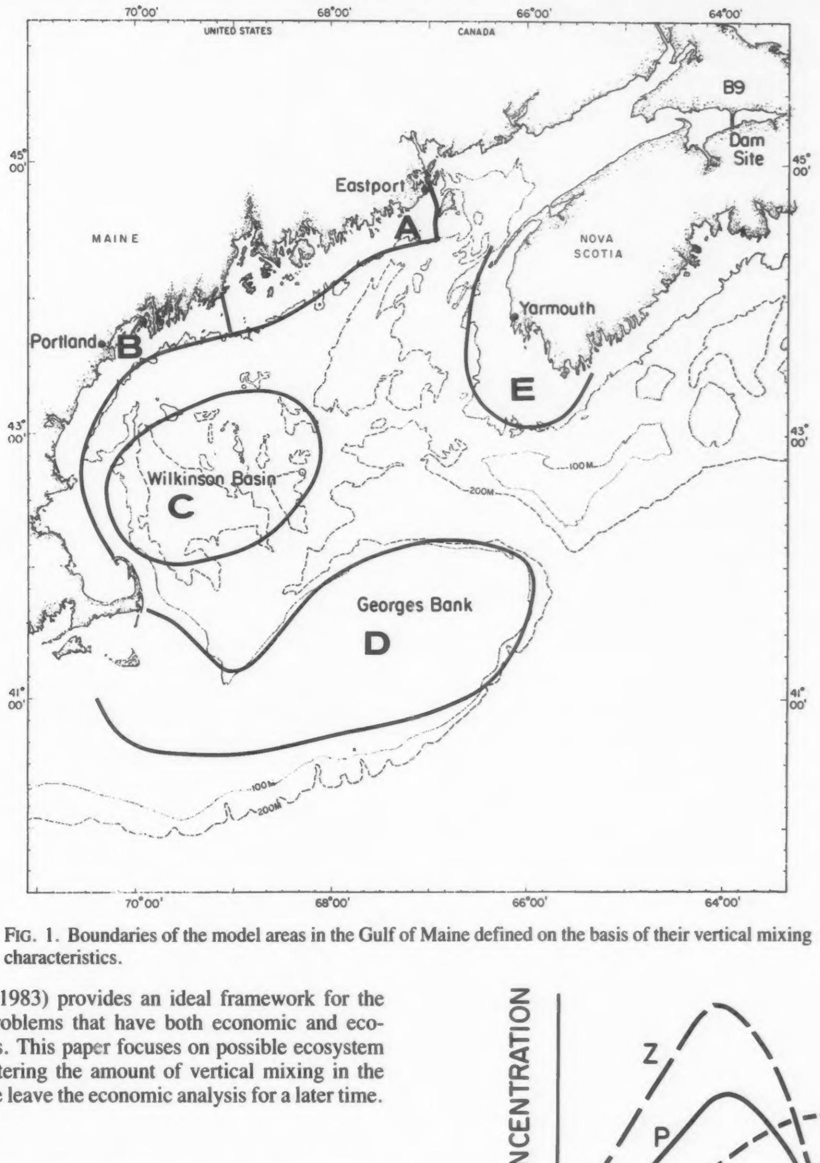

FIG. 1. Boundaries of the model areas in the Gulf of Maine defined on the basis of their vertical mixing characteristics.

by Odum (1971, 1983) provides an ideal framework for the examination of problems that have both economic and ecologic ramifications. This paper focuses on possible ecosystem changes due to altering the amount of vertical mixing in the Gulf of Maine. We leave the economic analysis for a later time.

Study Areas

Study area boundaries (Fig. 1) were defined on the basis of the distribution of vertical mixing off the Maine coast. The five areas outlined in Fig. 1 roughly conform to tidal mixing contours calculated by Garrett et al. (1978) using Greenberg's hydrodynamic model of the Gulf of Maine – Bay of Fundy system. Georges Bank and southwest Nova Scotia (areas D and E in Fig. 1) will not be analyzed here but will be considered in a later paper.

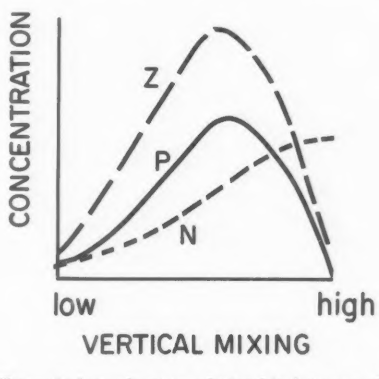

FIG. 2. Theoretical steady-state relationship between plankton ecosystem components and the extent of vertical mixing in the water column (redrawn from Riley 1965).

Bigelow (1927) first recognized the relationship between primary production and vertical mixing in the Gulf of Maine by plotting contours of vertical stability in the summer. Simpson and Hunter (1974) showed the importance of the ratio $\log_{10} h/u^3$ for delineating the well-mixed areas of a continental shelf from those that are stratified. In this expression, h is the water depth, and the energy available for vertical mixing is proportional to the cube of tidal velocity (u). Garrett et al. (1978) used a similar ratio of depth to tidal dissipation as calculated from the model of Greenberg (1979) to map the areas in the Gulf of Maine which remain well mixed throughout the year. They

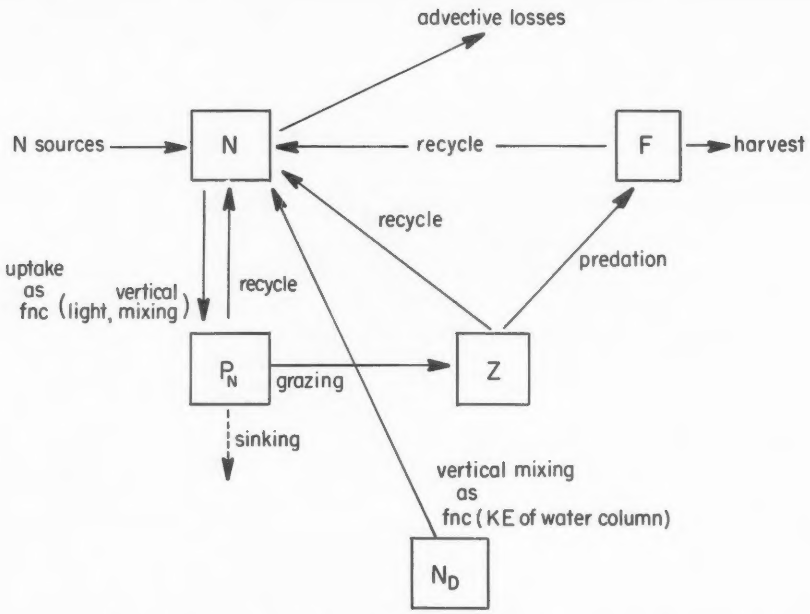

FIG. 3. Nitrogen budget box model of the marine ecosystem components.

showed that Georges Bank, Nantucket Shoals, and the mouth of the Bay of Fundy were the major, vertically mixed areas in the Gulf. Wind stress maps from Saunders (1977) show that a boundary may be defined between the eastern and western sections of the Maine coast, with the eastern coast receiving the higher amount of wind energy.

Yentsch and Garfield (1981) used satellite imagery to confirm and expand the previous work on vertical mixing and primary productivity in the Gulf of Maine. They observed that thermal fronts were a consistent feature of the Gulf of Maine from May to October. They noted that the model of Garrett et al. (1978) failed to simulate the observed well-mixed areas along the Maine coast. The transition depth between inshore vertically mixed areas and offshore stratified areas was underestimated by Garrett et al. (1978), and Yentsch and Garfield (1981) suggested that other factors (presumably wind energy) must be important. This significance of wind energy as well as tidal mixing is supported by Loder and Greenberg's (1986) application to the Gulf of various semi-empirical criteria for determining the extent of mixed areas.

Yentsch (1977, 1981) pointed out that where vertical mixing controls primary production, the competing effects of light limitation and nutrient supply contend for dominance. Turbulence generated by the wind and the tide acts both to stir nutrients up from depth (increasing primary production) and to mix phytoplankton cells down out of the euphotic zone (decreasing productivity). In a pioneering modeling paper, Riley (1965) showed how phytoplankton and zooplankton biomasses and dissolved nutrient concentration are governed by the amount of turbulence in the water column (Fig. 2).

The weight of present evidence leads to the conclusion that vertical mixing is the major factor controlling primary production in the Gulf of Maine from May through October. The amount of vertical mixing in the Gulf will almost certainly be changed by the construction of a dam across the Minas Basin. Therefore, the mathematical model used here to predict the possible ecological changes focuses on primary productivity in the surface waters of the Gulf of Maine. Phytoplankton growth is formulated in terms of a competition between light and nutrient limitations that is mediated by vertical mixing (Fig. 3). The effect of altered phytoplankton production on zooplankton and fish production is examined using food chain dynamics for three areas off the Maine coast which differ in their vertical mixing characteristics.

Modeling Methods

Energy circuit modeling (Odum 1971, 1983) was used to investigate the marine ecosystem dynamics in areas A, B, and C in Fig. 1. The models are represented visually by the diagrams in Fig. 4 and mathematically by the set of differential equations given in Table A.1 (see Appendix). The models were constructed so that the nitrogen budget (Fig. 3) was coupled with energy flow. Energy was converted to carbon using caloric equivalents and carbon was converted to nitrogen using a C:N ratio of 6.6:1 given by Redfield (1934). External forces that drive the system's behavior are solar radiation (J_I), wind (J_W), tide (J_T), and nitrogen input (J_N). The system components are the kinetic energy in the water column from the wind (W), the kinetic energy in the water column from the tide (T), dissolved limiting nutrient as nitrogen (N), zooplankton biomass (Z), and pelagic fish stock (F).

Phytoplankton productivity is represented as an instantaneous process (without energy storage) because the turnover of plant cells is much faster than other system components which depend on plants for nourishment (Odum 1983). Phytoplankton respiration and excretion are represented by box R in Fig. 4. Net primary production after losses to zooplankton grazing is represented by P_N, and can be thought of as the phytoplankton remaining in the water column. The formulation for P_N is like the J_R term (Table A.1, see Appendix). Both J_R and P_N are flow-controlled processes in which the fraction of resource that remains unused limits the increase of components or processes that depend on them for energy. For example, the albebo (J_R), which is the sum of reflection at the water surface and backscatter from the sea, may be altered by the quantity of phytoplankton in the water. Large albedos imply unused light energy which could provide a high potential for phytoplankton growth.

The water column is modeled as two layers. An upper mixed layer of average depth 50 m has aggregated nitrogen inputs from ocean currents, rain, and land runoff. Nitrogen in a deepwater layer (N_D) is the quantity of dissolved nutrient in a 50-m layer underlying the surface water layer. Mixing between the two layers is considered to be proportional to the product of tidal and wind energy in the water column and the nutrient gradient ($N_D - N$). The assumption is that the nutrient gradient will reflect the density gradient between the layers.

The transfer of energy from primary production through zooplankton to fish production is represented by a simple food chain (Fig. 4). Primary production is modeled to reflect the two opposing effects of vertical mixing on phytoplankton growth. Kinetic energy in the water column moves nitrogen toward the surface in proportion to the gradient between the surface mixed layer and the deepwater layer. At the same time, kinetic energy dilutes the phytoplankton in the surface waters by transporting them downward out of the euphotic zone. This process of dilution is modeled here as a mathematical division in the energy circuit diagram (Odum 1983).

The major difference between the coastal and offshore models shown in Fig. 4 is the relative importance of wind versus tidal mixing. In the models of the eastern and western Maine coast (Fig. 4a and 4b), both wind and tide have effects on primary production. The deepwater case (Fig. 4c) assumes that the effects of tide are negligible and that only wind mixing affects primary production. Differences between the models of the eastern and western Maine coast exist in the amount of nitrogen that is available in the surface and bottom layers, and in the quantities of wind and tidal energy input and storage.

Many of the storages, flows, and energy sources are available in the literature as annual average values. To use these mean values, it is necessary to assume that the ecosystem components exist in quasi-steady state over the period of interest. This assumption may be reasonable from May to October during which time primary production is largely controlled by vertical mixing. The values and references for each of the model pathways, forcing functions, and components are given in Table A.2 (Appendix). This model represents a first-order estimation of the ecological effects of an altered vertical mixing regime in parts of the Gulf of Maine.

Because of the simple trophic dynamics used in the model, zooplankton and fish variables actually represent aggregated components. For example, the zooplankton component includes both macro- and microzooplankton. In like manner, the fish compartment represents the total pelagic fish biomass including both commercial and noncommercial fish species. The actual fish production is undoubtably less than the value predicted here, since all zooplankton net production is assumed to support fish production. The value of fish yield or harvest (J_{11}) includes all commercially valuable pelagic species with the exception of menhaden.

The predicted change in pelagic fish yield (J_{11}) due to change in vertical mixing was evaluated by examining the response of the models in Fig. 4 to a step increase in the energy transferred to the mixing process from the wind or tide (flows J_T and J_W in Fig. 4). The models were first run to determine the steady-state solution. These steady-state values were then used to scale the values obtained in subsequent simulation runs that tested the model's response to perturbations in the wind and tidal energy. The model responded to a perturbation within a simulated year. New steady-state values of the model components and flows were recorded after a 10-yr run. The ratio of the new steady-state value of a model component (or flow) to its initial value was plotted against the ratio of the new wind or tidal energy level to its initial value. Plots of these nondimensional numbers in Fig. 5 and 6 represent the sensitivity of a model component or flow to changes in the forcing functions.

Results

The Maine east coast ecosystem (area A in Fig. 1) is a well-mixed area that has large inputs of both wind and tidal energy relative to the western portion of the Maine coast. The magnitude of the tidal energy available for turbulent mixing along the eastern coast is approximately 10 times greater than the available wind energy (compare J_W and J_T in Fig. 4a). The west coast ecosystem (area B in Fig. 1) is usually stratified in the summer but may become well mixed locally as the result of wind events (Yentsch and Garfield 1981). Tidal energy available for vertical mixing is four times greater than the wind energy for this section of the Maine coast (compare J_W and J_T in Fig. 4b). The offshore ecosystem (area C in Fig. 1) is strongly stratified in the summer months, and vertical mixing of the upper water column is dominated by the wind. Thus, J_T is negligible and tidal mixing is omitted from the model in Fig. 4c.

Fish Yield and Wind Energy

The yield of pelagic fish as a function of wind energy is shown in Fig. 5a–5c. The response of fish yield in the model of the eastern coast of Maine is different from the response of the western coast model (compare Fig. 5a and 5b). In the eastern area an increase in the amount of wind energy over the present annual average results in higher vertical mixing and a decrease in fish yield. Conversely, a decrease in the present amount of wind energy in this area brings about an increase in the pelagic fish yield (Fig. 5a). This response is caused by the large amount of both wind and tidal energy that is available for mixing along the eastern coast which insures a more than adequate supply of nutrients to support primary production. Any additional input of energy for mixing brings about a decrease in primary production by limiting the exposure of phytoplankton cells to light. It is interesting to note that even though there is 10 times more tidal energy than wind energy available for mixing along the east coast, an increase in wind energy still lowers plant growth. This is due to the fact that wind energy (which enters the system at the ocean surface) is approximately 10 times more efficient than tidal energy (which enters at the bottom) in mixing the euphotic zone (Garrett et al. 1978, see Appendix).

The response of fish yield along the west coast of Maine to changes in the present annual average wind energy is somewhat different (Fig. 5b). The western coastal area has roughly one fifth the tidal energy and one half the wind energy found along the eastern coast. Thus, when the wind energy falls far below the present value, fish yield decreases.

In the offshore ecosystem (Fig. 5c) where tidal mixing is negligible, the variation of fish yield with annual average wind

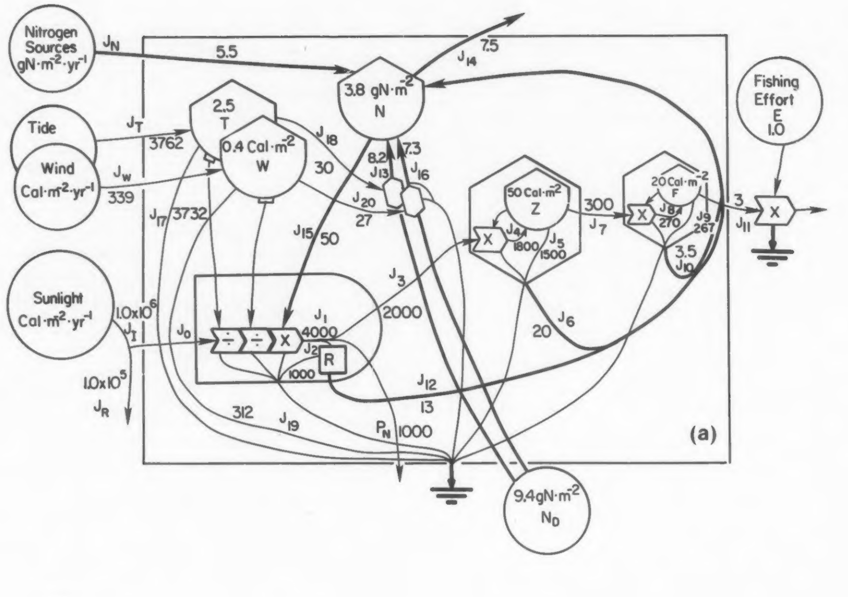
Nitrogen Sources gN·m^{-2}·yr^{-1}
J_N
5.5
7.5
J_{14}
3.8 gN·m^{-2}
N
Tide
Wind
Cal·m^{-2}·yr^{-1}
J_T
3762
J_W
339
2.5
T
0.4 Cal·m^{-2}
W
J_{18}
30
8.2
7.3
J_{13}
J_{16}
J_{20}
27
J_{17}
3732
J_{15}
50
Fishing Effort
E
1.0
50 Cal·m^{-2}
Z
300
J_7
20 Cal·m^{-2}
F
J_8
270
J_9
267
3
J_{11}
3.5
J_{10}
J_4
1800
J_5
1500
X
Sunlight
Cal·m^{-2}·yr^{-1}
1.0x10^6
J_I
J_0
J_1
4000
J_2
1000
R
J_3
2000
20
J_6
1.0x10^5
J_R
J_{12}
13
312
J_{19}
P_N
1000
(a)
9.4gN·m^{-2}
N_D
Nitrogen Sources gN·m^{-2}·yr^{-1}
J_N
5.5
7.5
J_{14}
1.9 gN·m
N
Tide
752
J_T
Wind
Cal·m^{-2}·yr^{-1}
179.8
J_W
0.5
T
0.2 Cal·m^{-2}
W
6
J_{18}
4.7
10.8
J_{13}
J_{16}
14.4
J_{20}
J_{17}
746
J_{15}
50
Fishing Effort
E
1.0
50 Cal·m^{-2}
Z
300
J_7
20 Cal·m^{-2}
F
J_8
270
J_9
267
3
J_{11}
J_{10}
3.5
J_4
1800
J_5
1500
X
Sunlight
Cal·m^{-2}·yr^{-1}
1.0x10^6
J_I
J_0
J_1
4000
J_2
1000
R
2000
J_3
20
J_6
1.0x10^5
J_R
13
J_{12}
165.4
J_{19}
P_N
1000
(b)
7.5 gN·m^{-2}
N_D

FIG. 4. Energy circuit diagrams representing the (a) eastern section of the Maine coast, (b) western section of the Maine coast, and (c) offshore waters of Wilkinson Basin. External energy sources and internal pathways are fluxes identified by J_i in the diagrams. Flows of matter are drawn in boldface and have units of g N · m^{-2} · yr^{-1}. Other numbered pathways are flows of energy with units of Cal · m^{-2} · yr^{-1} (see Table A.2, Appendix). Note: 1 Cal = 4183 J.

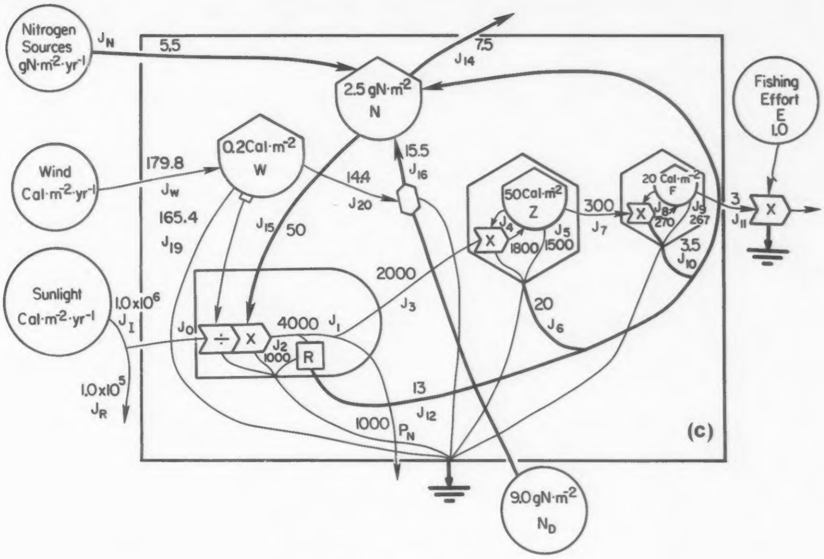

FIG. 4. (*Concluded*)

energy input is similar in form to that described for the west coast ecosystem (Fig. 5b). However, the optimum value of wind energy for fish production in the deepwater system is close to the present annual average value. Fish yield falls off rapidly when the wind energy is less than the optimum value for both the western coast and deepwater ecosystems. But when wind energy is greater than the optimum, there is only a gradual decline in fish yield.

Fish Yield and Tidal Energy

To estimate the effects of altered tidal mixing on potential fish production, both the Maine east and west coast ecosystems were simulated using wind energy equal to the average of the spring, summer, and fall winds given in Saunders (1977). In other words, we calculated the model response for the period from May to October when primary production is governed by vertical mixing. The lower amount of wind energy available from May to October allows the condition of nutrient limitation to appear for low values of tidal energy input; note the steep decline of fish yield as tidal energy is reduced (Fig. 5d and 5e).

The Maine west coast ecosystem responds differently from the east coast ecosystem to an increase in tidal mixing. A comparison of Fig. 5d and 5e demonstrates that tidal mixing keeps the west coast ecosystem productive by supplying nutrients to the phytoplankton. Even twice the present level of tidal mixing does not saturate the phytoplankton's requirement for nutrients. However, the east coast ecosystem is saturated with nutrients and the phytoplankton are light limited even at twice the present level of tidal mixing.

Ecosystem Production with Wind and Tidal Energy

The response of other ecosystem components and flows is shown in Fig. 6 by plotting the values of dissolved nitrogen (N), gross primary production pathway (J_1), and fish production pathway (J_8) against wind and tidal energy input. The amount of dissolved nutrient present in the surface layer is a monotonically increasing function of the energy available for vertical mixing. The model's predictions of the variability in fish production are seen to be a reflection of similar variations in gross primary production (Fig. 6). Relatively small percentage variations in plant production are transformed by the nonlinear dynamics of the trophic chain into larger percentage variations in fish production.

As a summary, Table 1 presents the sensitivity of potential fish yield to the expected variation in tide and solar radiation. For a 15−33% increase in the tidal mixing energy (based on tidal amplitude changes of 5−10% predicted by Greenberg (1979)), the model predicts a 7−12% increase in potential fish production along the Maine west coast. Little change is predicted for fish yield along the Maine east coast. The model is very responsive to a change in sunlight. A 3% variation in incident solar radiation gives greater than 10% variation in fish production. An examination of solar insolation data from Eastport and Portland, Maine (U.S. Department of Commerce, U.S. Weather Bureau 1950a, 1950b, 1951a, 1951b, 1952a, 1952b, 1953), indicates that a 3% variation in solar radiation over the Gulf commonly occurs from one year to another due to differences in cloud cover.

Discussion

The relationship between primary production and vertical mixing has been modeled previously by Steele (1958), Steele and Menzel (1962), Riley (1965), Yentsch (1981), and others. Riley (1965) used steady-state solutions to evaluate the influence of vertical mixing on the oceanic plankton in summer, and he pointed out that such an approach necessitates the debatable assumption that a quasi-steady state exists for the plankton from late spring to early fall. The obvious disadvantage of such a modeling approach applied to annual plankton and fish production is that the peak production during the spring and fall plankton blooms is ignored. Whether or not these peak productivity events play a role in the survival of fish larvae is

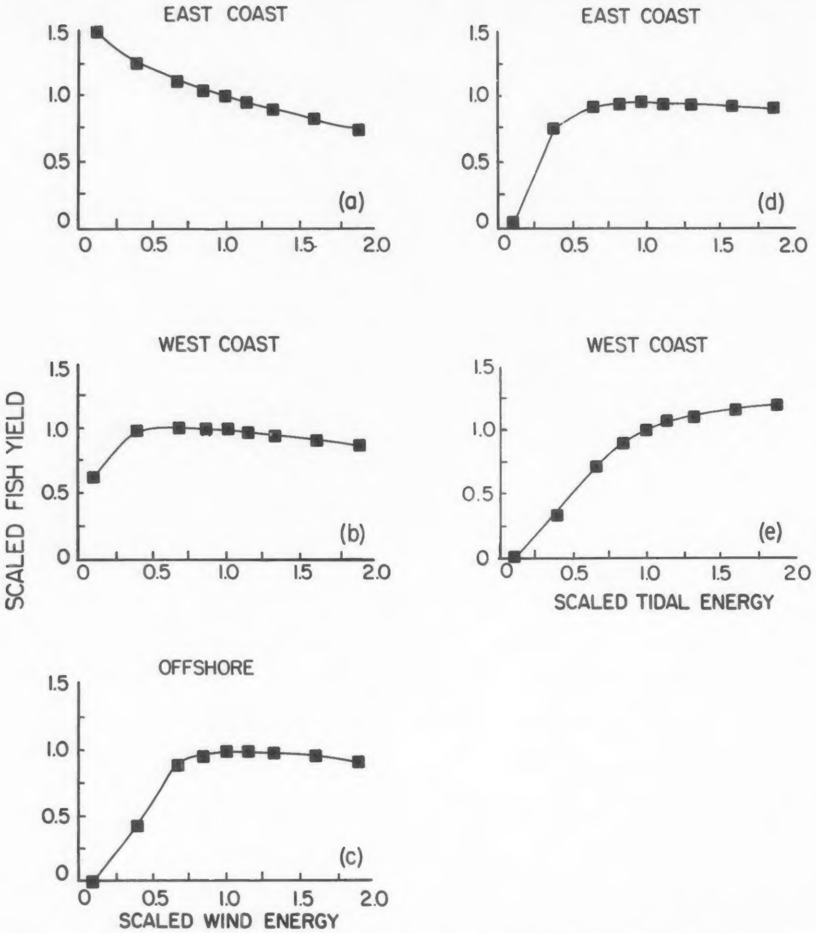

FIG. 5. Response of fish yield to changes in the annual average wind energy for the (a) Maine east coast, (b) Maine west coast, and (c) Wilkinson Basin. The response of fish yield to changes in tidal energy using May to October wind energy is shown for the (d) east coast ecosystem and (e) west coast ecosystem.

controversial (Sinclair and Tremblay 1984). Leaving aside questions of the importance of the spring and fall blooms, a first approximation of ecological effects caused by a shift in the major physical driving forces can be obtained under the quasi-steady state assumption.

Our model predictions are similar to the results of Riley's and Steele's models. Riley (1965) observed that while nutrient concentration in the upper mixed layer was a monotonically increasing function of vertical mixing, both phytoplankton and zooplankton had maxima as a function of vertical mixing (Fig. 2). The maxima for primary production (and hence, zooplankton, and fish production) as a function of vertical mixing in our model are the result of the dual effect of enhanced nutrient supply but reduced light availability to the phytoplankton. Both Maine coast ecosystems exhibit this maximum under certain conditions of wind and tidal mixing energy (Fig. 6). The model simulations demonstrate that the eastern coast of Maine is an area where the physical energies of wind and tide are presently high enough to supply the nutrient needs of the ecosystem even in the summer. This observation suggests that light is usually the limiting factor in this area. Gran and Braarud (1935) first presented evidence that light was the limiting factor for primary production in the Bay of Fundy and adjacent waters. The potential productivity of the western section of the Maine coast appears to be nutrient limited under summer breeze conditions but light limited for winds of greater force. The May to October wind energy over the deep waters of the Wilkinson Basin (0.4 on the abscissa of Fig. 5c) is lower than the optimum wind condition for maximum fish yield. Therefore, the nutrient supplied by wind mixing is the factor limiting primary production in the offshore waters during the summer. During the remainder of the year, wind mixing causes the phytoplankton to become light limited.

These results concerning light limitation are reinforced by the fact that the model is most sensitive to variations in solar energy. A comparison of changes in fish yield (Table 1) caused by variation in solar radiation and tidal mixing energy shows that it would be difficult to separate man-induced changes in

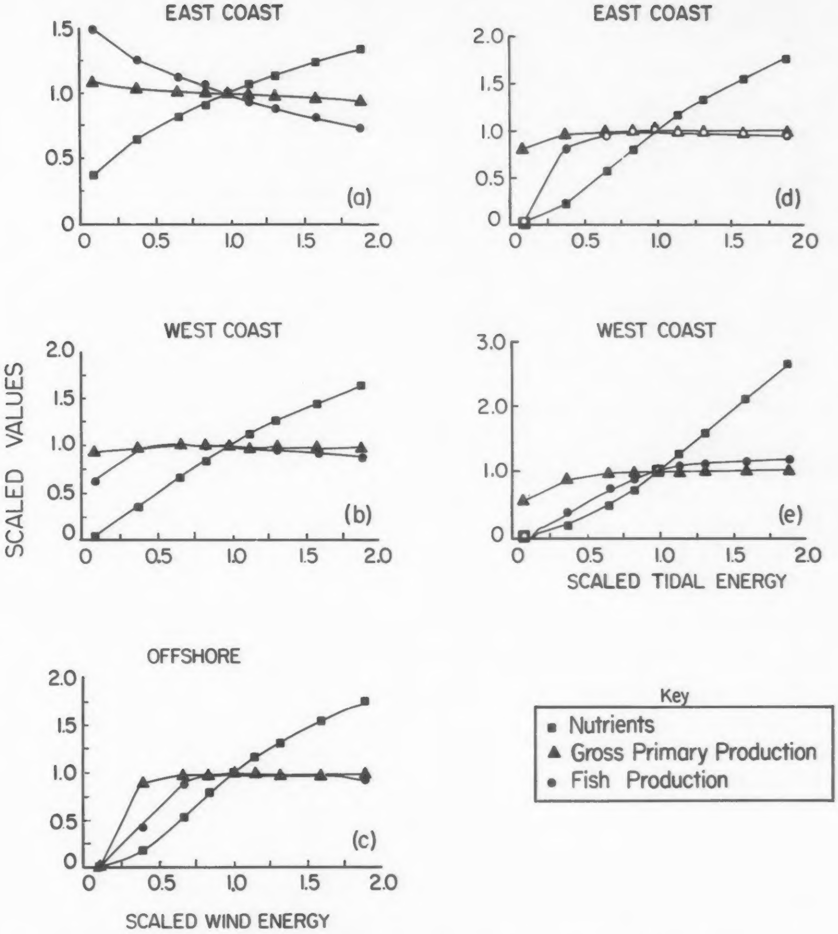

FIG. 6. Response of nutrients (N), gross primary production (J_1), and fish production (J_8) to changes in annual average wind energy for the (a) Maine east coast ecosystem, (b) Maine west coast ecosystem, and (c) offshore ecosystem in Wilkinson Basin. The response of these same quantities to changes in the tidal energy given May to October wind energy is shown for the (d) east coast ecosystem and (e) west coast ecosystem.

ecosystem productivity from changes due to climatic variability. Man-induced changes in the local climate are not evaluated in this study. Lower surface water temperatures caused by increased vertical mixing could cause an increase in the occurrence of fog along the Maine coast. Therefore, the amount of solar radiation available to support ecosystem productivity would be decreased. In addition, this analysis did not evaluate the effects of increased turbidity caused by increased sediment resuspension in areas of shoal water and/or high tidal current speed. Finally, the response of fish yield depends strongly on the value assigned to the wind. Year to year changes in the weather are known to dramatically influence fisheries (Cushing 1982). These unevaluated indirect effects of dam construction were assumed to be secondary to the direct effects of increased vertical mixing on ecosystem productivity. Additional research is needed to determine whether or not this assumption is valid.

TABLE 1. Sensitivity analysis of the effects of variation in solar radiation and tidal energy on potential fish yield off the Maine coast. The model uses wind conditions representative of the period from May to October.

Energy input	% change	% change in fish yield		
		East coast	West coast	Offshore
Tide	33	−0.5	12.2	—
	15	−0.03	7.1	—
Sun	3	13.4	10.7	14.5
	−3	−13.5	−11.9	−16.5

The models presented here are not intended to be a final statement of the potential effects of increased vertical mixing on ecosystem productivity in the Gulf of Maine. The percentage changes predicted by the model are less significant than the overall response of the ecosystem to changes in mixing energy. Additional research is needed to make more refined estimates of the ecological impacts of tidal power development upon the entire Gulf of Maine region. An interdisciplinary, international field program guided by plausible ecological models is needed to collect relevant baseline data in the Gulf of Maine if plans for Fundy tidal power development proceed further.

In summary, we investigated the factors controlling primary production and (in an aggregate sense) potential pelagic fish production in the Gulf of Maine. Light intensity was identified as the most probable factor limiting summer primary productivity (and ultimately fish production) along the eastern coast of Maine. In contrast, phytoplankton production along the western coast of Maine is probably limited by nutrients during the summer. Using Greenberg (1979) for predictions of tidal amplitude increase as a result of the construction of a Fundy tidal power plant, the impact of changes in the energy available for vertical mixing on potential pelagic fish production was estimated. The model predicts that the potential for fish production from May to October along the eastern coast of Maine will be unaffected by the predicted increase in tidal amplitude. Fish production along the western section of the Maine coast may be expected to increase by 7−12%. In offshore waters where tidal energy contributes a negligible fraction of the energy for mixing, fish production would be unaffected by a change in the tidal amplitude. Natural climatic variation is predicted to have as large an impact on potential fish production as man-induced variation in vertical mixing associated with the construction of a tidal power dam across the Minas Basin in the Bay of Fundy.

Acknowledgements

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Appendix

Wind Energy Calculations

Seasonal wind stresses over the Gulf of Maine were obtained from Saunders (1977). The annual average wind stress was 0.625 dynes·cm^{-2} for the eastern Maine coast and 0.41 dynes·cm^{-2} for the western Maine coast and Wilkinson Basin. The relationship between shear stress and wind velocity is given by

$$(1)\quad \tau = \rho C_D (U_{10})^2$$

where ρ is the air density given a value of 1.2×10^{-3} g·cm^{-3}, C_D is the drag coefficient assumed to be 1.0×10^{-3} for wind velocities around 5 m·s^{-1} (Smith and Banke 1975), and U_{10} is the wind velocity 10 m above the water surface.

Substituting the shear stress values given above into equation (1), we obtain an annual average wind velocity of 584 cm·s^{-1} for the western coast and 721 cm·s^{-1} for the eastern coast. Multiplying average shear stress by the average velocity gives an average available energy of 239 ergs·s^{-1}·cm^{-2} for the western area and 451 ergs·s^{-1}·cm^{-2} for the eastern area. Converting the result to kilocalories (Cal) per square metre per year gives 1798 Cal·m^{-2}·yr^{-1} of wind energy available to the western area and 3391 Cal·m^{-2}·yr^{-1} available along the eastern coast. Using similar logic and summer wind stresses of 0.33, 0.18, and 0.22 dynes·cm^{-2} for the east coast, west coast, and offshore areas, respectively, we obtain summer wind energy inputs of 1273 Cal·m^{-2}·yr^{-1} for the east coast area, 538 Cal·m^{-2}·yr^{-1} for the west coast area, and 709 Cal·m^{-2}·yr^{-1} for the offshore Wilkinson Basin.

Richman and Garrett (1977) estimate that 4–9% of the available wind energy is transferred to the mixed layer. Since we do not wish to underestimate the importance of wind mixing in this study, we assume an upper bound of 10% or 179.8 Cal·m^{-2}·yr^{-1} for the western area (J_W in Fig. 4b and 4c) and 339 Cal·m^{-2}·yr^{-1} for the eastern area (J_W in Fig. 4a). Richman and Garrett (1977), using data from Kato and Phillips (1969), estimated that 6–8% of the energy transferred to the mixed layer goes into vertical mixing. Using a value of 8%, the energy that goes into vertical mixing is 27 Cal·m^{-2}·yr^{-1} (J_{20} in Fig. 4a) for the eastern area and 14.4 Cal·m^{-2}·yr^{-1} (J_{20} in Fig. 4b and 4c) for the western and offshore areas.

The mean value of wind energy in the mixed layer at any given time is calculated from the average value of wind energy transferred to the mixed layer per day (J_W), with an average decay time ($1/k$) of 0.42 d obtained from Klein and Coantic (1981). The wind energy (W) may be described by the following differential equation:

$$(2)\quad dW/dt = J_W - kW.$$

The integrated equation for W is

$$(3)\quad W = (J_W/k)\,(1 - e^{-kt}) + W_0 e^{-kt}.$$

At steady state, W approaches an asymptote of J_W/k equal to 0.4 Cal·m^{-2} for the eastern coast (W in Fig. 4a) and 0.20 Cal·m^{-2} for the western coast and offshore area (W in Fig. 4b and 4c).

Tidal Energy Calculations

A mean tidal kinetic energy in the water column of 1 J·cm^{-2} for the east coast and 0.2 J·cm^{-2} for the west coast is taken from Greenberg (1979). Converting to kilocalories per square metre, one obtains 2.5 and 0.5 Cal·m^{-2} for T in Fig. 4a and 4b, respectively.

The mean frictional dissipation of tidal energy along the eastern portion of the Maine coast is 5 W·cm^{-2} from Greenberg (1979). A value of 1 W·cm^{-2} for the western coastal area is obtained from the same source. Converting to kilocalories per square metre per year, we find that 3762 Cal·m^{-2}·yr^{-1} (J_T in Fig. 4a) and 752 Cal·m^{-2}·yr^{-1} (J_T in Fig. 4b) of tidal energy is transferred to the water column along the eastern and western sections of the Maine coast, respectively.

Garrett et al. (1978) estimated that 0.3% of frictionally dissipated tidal energy goes into breaking down vertical stratification at tidal frontal boundaries in the Gulf of Maine. This value provides a minimum estimate of the amount of frictionally dissipated tidal energy that contributes to the vertical transport of nutrients and organisms. In shoal waters where $h/u^3 \ll 70$ m^{-2}·s^3, a larger percentage of energy can go into transport because a smaller percentage of the tidal energy is necessary to break down slight vertical stratification. Since we do not wish to overestimate the importance of tidal mixing in our model, we assume that 0.8% of the tidal energy that is frictionally dissipated in the nearshore waters (0–100 m depth) goes into vertical transport of nutrients and organisms. Our choices lead to the observation that wind energy is 10 times more efficient than tidal energy in mixing the waters in the Gulf of Maine. Multiplying this mixing efficiency by J_T for the east and west coastal areas gives values for J_{18} of 30 and 6 Cal·m^{-2}·yr^{-1}, respectively, of tidal energy that goes into mixing the two layers in the model.

TABLE A.1. Equations describing the models in Fig. 4. The full set of equations applies to the models in Fig. 4a and 4b. Removal of the terms in boldface type gives the equations for the model in Fig. 4c. See Table A.2 for definitions of component variables (Q) and pathway flows (J) where $J_i = k_i Q$ and k_i is a transfer coefficient.

$$(1)\quad J_R = \frac{J_I}{1 + k_0 N/W\mathbf{T}}$$

$$(2)\quad P_N = \frac{k_1 N J_R}{W\mathbf{T}(1 + k_2 + k_3 Z)}$$

$$(3)\quad dZ/dt = k_4 Z P_N - k_5 Z - k_7 Z F$$

$$(4)\quad dF/dt = k_8 Z F - k_9 F - k_{11} F E$$

$$(5)\quad dN/dt = J_N + k_{16}\,(N_D - N)W + \mathbf{k_{13}\,(N_D - N)T} + k_{12} P_N + k_6 Z + k_{10} F - k_{15} J_R N/W\mathbf{T} - k_{14} N$$

$$(6)\quad \mathbf{dT/dt = J_T - k_{17} T - k_{18}\,(N_D - N)T}$$

$$(7)\quad dW/dt = J_W - k_{19} W - k_{20}\,(N_D - N)W$$

TABLE A.2. Definition and documentation of pathways, storages, and forcing functions presented in Fig. 4.

Symbol	Description	References and assumptions
	Forcing functions	
J_I	Solar radiation at water surface (Cal·m^{-2}·yr^{-1})	List 1971
J_N	Nitrogen transport in rain, runoff, and currents (g N·m^{-2}·yr^{-1})	Schlitz and Cohen 1984
J_T	Mean frictional dissipation of tidal energy (Cal·m^{-2}·yr^{-1})	Greenberg 1979; see Appendix
J_W	Wind energy transferred to the water surface (Cal·m^{-2}·yr^{-1})	Saunders 1977; see Appendix
J_R	Surface albedo (Cal·m^{-2}·yr^{-1})	Von Arx 1962
J_N	Nitrogen in the layer from 50 to 100 m (g N·m^{-2})	Apollonio and Applin 1972; Kilpatrick et al. 1979
E	Fishing effort	Assumed constant at 1974 level, see J_{11}
	Component variables (Q)	
T	Tidal kinetic energy storage in the water column (Cal·m^{-2})	Greenberg 1979; see Appendix
W	Wind kinetic energy storage in the water column (Cal·m^{-2})	Klein and Coantic 1981; see appendix
N	Nitrogen in the mixed layer (g N·m^{-2})	Apollonio and Applin 1972; Kilpatrick et al. 1979
Z	Zooplankton (Cal·m^{-2})	Cohen et al. 1982
F	Pelagic fish (Cal·m^{-2})	Assume that mean herring stock (Fogarty and Clark 1983) is 2/3 of pelagic fish biomass
P_N	Net primary production after grazing losses (Cal·m^{-2}·yr^{-1})	By difference ($J_1 - J_2 - J_3$)
R	Site of phytoplankton metabolic processes	
	Pathway flows (J)	
J_0	Solar energy absorbed by the system (Cal·m^{-2}·yr^{-1})	By difference ($J_I - J_R$)
J_1	Gross primary production (Cal·m^{-2}·yr^{-1})	Net primary production (NPP) from Cohen et al. 1982 plus 25% for respiration and excretion
J_2	Phytoplankton respiration and excretion (Cal·m^{-2}·yr^{-1})	Steemann Nielson and Hansen 1959, 10% of NPP; Hellebust 1965, 15% of NPP
J_3	Zooplankton ingestion (Cal·m^{-2}·yr^{-1})	Calculated as the sum of respiration excretion and production (Cohen et al. 1982) divided by assimilation
J_4	Zooplankton assimilation (Cal·m^{-2}·yr^{-1})	90% of ingestion (Conover 1966)
J_5	Zooplankton respiration and excretion (Cal·m^{-2}·yr^{-1})	Schlitz and Cohen 1984
J_6	Remineralization from zooplankton (g N·m^{-2}·yr^{-1})	Schlitz and Cohen 1984
J_7	Fish ingestion (Cal·m^{-2}·yr^{-1})	Assume all secondary production is ingested
J_8	Fish gross production (Cal·m^{-2}·yr^{-1})	Assume 90% of ingestion (Blaxter and Hunter 1982)

TABLE A.2. (*Concluded*)

Symbol	Description	References and assumptions
J_9	Fish respiration, excretion, and natural mortality ($\mathrm{Cal \cdot m^{-2} \cdot yr^{-1}}$)	By difference ($J_8 - J_{11}$)
J_{10}	Remineralization from fish ($\mathrm{g\ N \cdot m^{-2} \cdot yr^{-1}}$)	From J_9 using C:N = 6.6
J_{11}	Fish yield ($\mathrm{Cal \cdot m^{-2} \cdot yr^{-1}}$)	U.S. Department of Commerce, NOAA, NMFS 1974 (Maine landings)
J_{12}	Plant remineralization ($\mathrm{g\ N \cdot m^{-2} \cdot yr^{-1}}$)	From J_2 using C:N = 6.6
J_{13}	Nitrogen transport from tidal mixing ($\mathrm{g \cdot N \cdot m^{-2} \cdot yr^{-1}}$)	By difference prorated as $J_{18}/(J_{18} + J_{20})$
J_{14}	Advective nitrogen losses ($\mathrm{g \cdot N \cdot m^{-2} \cdot yr^{-1}}$)	Schlitz and Cohen 1984
J_{15}	Phytoplankton uptake ($\mathrm{g \cdot N \cdot m^{-2} \cdot yr^{-1}}$)	Schlitz and Cohen 1984
J_{16}	Nitrogen transport from wind mixing ($\mathrm{g \cdot N \cdot m^{-2} \cdot yr^{-1}}$)	By difference prorated as $J_{20}/(J_{18} + J_{20})$
J_{17}	Tidal energy dissipated in process other than mixing ($\mathrm{Cal \cdot m^{-2} \cdot yr^{-1}}$)	By difference ($J_T - J_{18}$)
J_{18}	Tidal energy used in mixing ($\mathrm{Cal \cdot m^{-2} \cdot yr^{-1}}$)	0.8% of J_T (Garrett et al. 1978; see Appendix)
J_{19}	Wind energy dissipated in processes other than mixing ($\mathrm{Cal \cdot m^{-2} \cdot yr^{-1}}$)	By difference ($J_W - J_{20}$)
J_{20}	Wind energy used in mixing ($\mathrm{Cal \cdot m^{-2} \cdot yr^{-1}}$)	8% of J_W (Richman and Garrett 1977; see Appendix)

Optimal Effort Allocation Among Competing Mixed-Species Fisheries, Subject to Fishing Mortality Constraints

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A linear programming (LP) approach to effort allocation among two or more fisheries (fleets) exploiting several common species/stocks is described and applied to otter trawl fisheries exploiting demersal fish stocks on Georges Bank (northeastern United States). Total instantaneous fishing mortality on a particular species (*i*) is computed as the linear summation of fishing mortalities generated by each fishery (*j*):

$$F_{i\cdot} = \sum_{j} q_{ij} \cdot f_j$$

where f_j is the amount of standardized fishing effort exerted in fishery *j* and q_{ij} is the catchability coefficient for species *i* taken in fishery *j*. Mortality on species *i* due to both directed fishing and by-catch can thus be accounted for in the q_{ij}'s. Optimal allocation of effort among the *j* fisheries may be considered a minimization problem (minimize Σf_j), subject to the constraints that fishing mortality rates on particular species are maintained at, above, or below certain predefined levels. Fishing mortality goals for individual species can be based on various biological and/or economic criteria: fishing mortality rates that prevent growth or recruitment overfishing, or that optimize productivity from predator–prey systems. Other constraints in the LP model may be included to modify optimal solutions based on various economic and social considerations (e.g. protection of certain fisheries). Sensitivity analyses indicate the general infeasibility of maintaining relatively high or low fishing mortality rates on ubiquitously distributed species, while moderately fishing species with more discrete distributions, due to by-catch considerations.

Une approche par programmation linéaire (PL) à la répartition des efforts de pêche entre deux ou plusieurs flottilles exploitant les mêmes espèces ou stocks est décrite et appliquée à la pêche au chalut de stocks de poissons démersaux du banc de Georges (nord-est des États-Unis). La mortalité instantanée totale due à la pêche d'une espèce donnée (*i*) est calculée comme étant la somme linéaire des mortalités due à la pêche de chaque flottille (*j*) :

$$F_{i\cdot} = \sum_{j} q_{ij} \cdot f_j$$

où f_j est l'effort de pêche normalisé exercé dans la pêche *j* et q_{ij} est le coefficient du potentiel de capture de l'espèce *i* pêchée par *j*. La mortalité de l'espèce *i* due aux prises directes et aux prises accessoires peut donc être représentée par q_{ij}. La répartition optimale de l'effort de pêche entre les flottilles *j* peut être traitée comme un problème de minimisation (minimisation de Σf_j) où les taux de mortalité dues à la pêche d'espèces données sont maintenus, supérieurs ou inférieurs à certains niveaux prédéfinis. Les objectifs de mortalité due à la pêche d'espèces données peuvent être basés sur divers critères biologiques ou économiques : taux de mortalité due à la pêche qui empêchent la croissance, ou la surpêche du recrutement, ou qui optimisent la productivité de systèmes prédateurs – proies. D'autres contraintes peuvent être incluses au modèle PL afin de modifier les solutions optimales en fonction de diverses considérations économiques et sociales (p. ex., la protection de certaines pêches). Des analyses de sensibilité montrent l'impossibilité générale de maintenir des taux de mortalité due à la pêche relativement élevés ou faibles pour des espèces à distribution ubiquiste tout en effectuant une pêche modérée d'espèces à distribution plus distincte, ceci à cause des prises accessoires.

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Effective management of multispecies fishery resources involves consideration not only of biological interactions, but also of operational constraints imposed by mixed-species harvesting (Mercer 1982). Failure to recognize limitations due to technological interrelationships (Pope 1979) on the management of mixed-species fisheries may have obvious negative effects: wasteful discarding at sea of species whose annual quota has been exceeded but is caught with other nonprohibited species, surreptitious landings (both in terms of quantities and reported species composition), and failure to achieve optimum physical or economic yields from one or more constituent species (Silvert and Dickie 1982).

In this study we evaluate the potential feasibility of managing mixed-species fisheries based on relationships of fishing effort to mortality rates. Rather than determining optimum catch quota constraints for various directed fisheries (Gundermann et al. 1974; Fukuda 1976; Brown et al. 1979; Overholtz 1985), a proposed linear programming (LP) formulation seeks to optimize fishing effort levels among fisheries such that total instantaneous fishing mortality rates on the species considered are held at predefined objective levels. Given that two or more mixed-species fisheries exploit the same species complex (but catch differing proportions of each species), the objective of the approach is to determine the optimum (in this case the minimum) amount of standardized effort generated in all fisheries combined, and the appropriate allocation among the component fisheries. Constraints on fishing effort levels are specified mortality rates for each species which may be determined under various criteria. In addition, other constraints modifying various economic consequences of the optimum effort pattern on particular segments of the industry can be included (e.g. minimum levels of effort that must be maintained in particular fisheries).

Several studies have addressed the problem of quota allocation among various mixed-species fisheries competing for the same resources, with individual species quotas as limiting factors (Gundermann et al. 1974; Fukuda 1976; Brown et al. 1979; Overholtz 1985). Total catch of a species was the sum from targeted fisheries, plus incidental catches (by-catch) from fisheries directed at other species. Total catch from directed fisheries for a species was thus limited by the degree of by-catch in other fisheries, such that an overall species quota could not be exceeded. The problem was assessed as one of constrained optimization; LP techniques (Taha 1978) were applied to solve for optimum levels of directed fishing on each species, by fishery (in several of these studies fisheries were defined by target species and fishing nation).

Application of LP to quota allocation problems for mixed-species fisheries, however, has several drawbacks. Optimum solutions for directed harvest levels are sensitive to proportions of incidental catch taken in each fishery (i.e. by-catch ratios). In all the aforementioned studies, by-catch ratios were based on landings from the various fisheries for years previous to the one for which quotas are projected. These ratios may even be several years old because of logistical problems in assembling necessary data. The relative proportions of species taken in mixed-species fisheries can change rapidly over time, even within a year (e.g. recruitment to the fishery of a strong year class); in such cases, setting of overall catch quotas, and their allocation by fishery, based on previous by-catch ratios, may thus result in ineffective management. If a strong but unanticipated year class of an important species was to recruit during the fishing season, under the quota allocation scheme, not only would directed fisheries exhaust their allocations of the species before the end of the season, but by-catch of the species may limit activities in fisheries directed at other species. This may result in the significant detrimental consequences previously mentioned, and could restrict fishing mortality on the strong year class below levels considered optimum, based on various biological and economic criteria.

In general, the aim of quota-based fishery regulation is to control fishing mortality on one or more species. Quotas may further be divided among seasons and user groups to effect other management objectives. However, given the difficulties with catch quota regulations as a device for controlling mortality in multiple-species fisheries, a strategy more robust to vagaries in the abundance of various populations and less dependent on precise predictions of annual stock sizes seems desirable. Such a strategy might involve managing the amount and areal distribution of fishing effort based on explicit consideration of the relationship of fishing effort expended in each of the mixed-species fisheries considered, and resulting total fishing mortality rates generated on the species complex.

The proposed effort-oriented approach is illustrated for several mixed-species otter trawl fisheries exploiting demersal fish stocks in the Georges Bank region off the northeast United States (Murawski et al. 1983).

Adaptation of the LP Model

In the present context, LP can be considered a systematic procedure for optimally allocating limited resources among several optional activities that share them (Taha 1978). The objective of the model is to determine the level of each activity that optimizes (maximizes or minimizes) the combined output of all activities, subject to the specified resource limitations. The LP model can be extended to the problem of controlling fishing mortality in mixed-species, multifishery situations by setting specific mortality rates on species of interest as constraints, and assuming that mortality is functionally proportional to fishing effort:

$$F_{i\cdot} = \sum_{j=1}^{m} q_{ij} \cdot f_j$$

where f_j = standardized fishing effort exerted in fishery j ($j = 1,2,3,\ldots,m$), q_{ij} = proportionality constant (catchability coefficient) that is species and fishery dependent, and $F_{i\cdot}$ = instantaneous fishing mortality rate on species i due to all m fisheries. In this context the objective of the analysis is to minimize Σf_j subject to certain fishing mortality rate goals for each species considered. Fishing mortality goals may be either equalities (e.g. F on cod = 0.3) or inequalities (e.g. F on haddock $<$ or $>$ some value).

Based on various biological and economic criteria, it may be desirable to maintain mortality rates at specific levels for several species, allow mortality rates for others to exceed particular levels, and constrain rates on still other species to less than particular values.

The parameter q_{ij} determines the fishing mortality generated on species i from a unit of fishing effort in fishery j. By varying the amount of fishing effort exerted in each of the j fisheries, it may be feasible to simultaneously fulfill the mortality rate objectives for all species considered. However, not all combinations of fishing mortality objectives may be possible simultaneously. If, for example, two species are caught in equal proportions by several mixed-species fisheries, it may not be possible to constrain mortality rates at a low level for one species and a substantially higher level for the other.

Fishing mortality objective for the various component species of mixed-species fisheries may be based on a number of criteria. Most often, target mortality rates for fishery populations are specified in relation to maximizing yield per recruit (preventing growth overfishing) or, as in the case of anadromous species, fishing mortality rates are constrained to prevent recruitment overfishing. For demersal fish species, the most common mortality objectives are rates resulting in maximum yield per recruit ($F_{\max}$) for a particular mesh size, or mortality rates that result in a marginal increase in yield per recruit of 10% of that from a lightly exploited fishery ($F_{0.1}$, Gulland and Boerema 1973).

Depending on the fishery system considered, it may be desirable to control mortality rates on the species based on other objectives. Biological interactions (i.e. predator–prey relationships) among fishery populations may dictate that in order to maximize the abundance of particular desirable species, fishing mortality on certain predators be maintained at a relatively high level. Sparre (1979) analyzed the potential impacts of reducing fishing mortality of North Sea cod (*Gadus morhua*) on the abundance of herring (*Clupea harengus*), which is both a prey of cod, and is itself caught for human consumption. Sparre demonstrated that by substantially reducing F on cod from the current high level (far in excess of $F_{\max}$), consumption of herring by the cod stock would increase, thereby reducing herring yields to fishermen. The increased consumption of herring was due both to the increased abundance and average size of cod as an effect of reduced cod F.

Still other fishing mortality objectives may relate to economic criteria, such as the relative values of species caught (Silvert and Dickie 1982). Thus, by focusing on explicit fishing mortality objectives for the various species harvested by several mixed-species fleets, the LP model can conceptually be used to analyze allocation problems based on diverse fishing mortality objectives for the various constituent species.

Fishing mortality rates, however, are not the only real-world constraints in multiple-fishery allocation problems. The costs of operation in each mixed-species fishery may be different (e.g some may be more distant from port and thus require higher variable costs to pursue). The value of landings from each fishery may vary greatly, based on the species composition of landings for each, and the relative values of the species. Thus, economics associated with each fishery may be quite different. Furthermore, there may be substantial economic and social penalties associated with an effort allocation scheme different from status quo (Shepherd and Garrod 1982).

Socioeconomic factors may be accounted for in the LP model either by modifying the constraints (resource limitations) or by redefining the objective function. If, for example, the optimal effort solution results in substantial shifts and/or reductions of effort among fisheries, it may be desirable to limit the amount the LP solution differs from status quo. This may be accomplished by fixing the minimum amount of effort in selected fisheries as a percentage of the overall effort total, or by assigning effort values to particular fisheries a priori (obviously this cannot be done for all fisheries, since the solution would then be determined). Optimal solutions may be gradually phased in to minimize negative economic and social impacts. This could be accomplished by incrementally reducing (or increasing) F constraints on particular species over a series of fishing seasons until "optimal" levels are achieved.

The objective function, as currently formulated, can be specified to optimize (maximize or minimize) variables other than fishing effort totals. The objective of minimizing total effort is actually a surrogate for a more complex function of economic efficiency, including fixed and variable costs and profit from the various fisheries. Another parameter in the objective function (C_j) can be used to weight the quantity of effort in each fishery by several economic performance measures (i.e. optimize $\sum_j C_j f_j$). The C_j's may represent the variable costs, gross expected revenue, or net profit from a day's activity in fishery j. The objective function can thus be defined to minimize variable costs or maximize profit under both biological (fishing mortality) and other socioeconomic constraints.

TABLE 1. Values of $F_{0.1}$[a] and $F_{\max}$[b] for four demersal fish stocks in the Georges Bank region off the northeast United States for different otter trawl cod-end mesh sizes. Calculations are based on the Thompson and Bell (1934) yield per recruit analysis. Input data are given in Murawski (1984).

Species	Mesh size (mm)	$F_{0.1}$	$F_{\max}$
Atlantic cod	102	0.1299	0.2001
	127	0.1441	0.2324
	140	0.1545	0.2588
	152	0.1659	0.2888
Haddock	102	0.2041	0.3785
	127	0.2329	0.4843
	140	0.2480	0.5550
	152	0.2628	0.6321
Yellowtail flounder	102	0.1930	0.2895
	127	0.2153	0.3343
	140	0.2299	0.3640
	152	0.2472	0.4001
Winter flounder	102	0.1958	0.3001
	127	0.2149	0.3423
	140	0.2333	0.3893
	152	0.2566	0.4568

[a] Instantaneous fishing mortality rate generating a marginal increase in yield per recruit of 10% of that from a lightly exploited fishery.

[b] Instantaneous fishing mortality rate resulting in maximum yield per recruit.

Example

An application of the LP model formulated above is illustrated for a mixed-species fishery system in the Georges Bank region off the northeast United States (Murawski et al. 1983; Murawski 1984). Four demersal species (Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; yellowtail flounder, *Limanda ferruginea*; and winter flounder, *Pseudopleuronectes americanus*) annually yield in aggregate about 90% of demersal fish landings from the region. Most of the landings (over 80%) are derived by otter trawl. Murawski et al. (1983) defined six operationally distinct otter trawl fisheries in the region, based on geographic and seasonal differences in percentage occurrence of the four major fish species as well as 23 other species or groups. Catchability coefficients by species and fishery were estimated by assuming that the proportion of total fishing mortality attributable to a fishery was equal to the fraction of total landings of a species derived from that fishery. If 50% of the catch of species i was derived from fishery j, then it was assumed that half of the overall species F was attributable to that fishery (Murawski 1984). Dividing these

TABLE 2. Linear programming solutions of optimal total fishing effort, and allocation among six mixed-species otter trawl fisheries in the Georges Bank region. Effort is constrained so that specified mortality rates are maintained on Atlantic cod, haddock, yellowtail flounder, and winter flounder. Analyses are presented for four otter trawl cod-end mesh sizes.

Mesh size (mm)	Fishing mortality constraints[a]	Optimum total effort[b]	% allocation by fishery					
			1	2	3	4	5	6
102	$F_{0.1}$	4 251	0.0	7.1	20.4	50.3	22.2	0.0
127	$F_{0.1}$	4 687	0.0	9.3	18.2	46.1	26.3	0.0
140	$F_{0.1}$	5 043	0.0	8.2	19.4	44.7	27.7	0.0
152	$F_{0.1}$	5 555	0.0	7.6	20.0	50.7	21.6	0.0
102	F_{max}	6 839	0.0	5.6	18.2	37.2	39.0	0.0
127	F_{max}	8 028	0.0	4.6	17.2	30.9	47.3	0.0
140	F_{max}	9 134	0.0	3.1	18.0	28.4	50.5	0.0
152	F_{max}	10 347	0.0	2.3	20.5	26.2	51.0	0.0

[a] $F_{0.1}$ and F_{max} values for the four species and four mesh size options are given in Table 1.

[b] Equivalent days fished by otter trawlers, standardized by vessel size class and fishing gear type.

"partial" F's by the amount of standardized effort necessary to generate them resulted in estimates of q_{ij}. During 1979, total standardized fishing effort for all fisheries combined was about 19.8 thousand vessel days. Estimated fishing mortality rates for the four species during 1979 were as follows: Atlantic cod = 0.6, haddock = 1.0, yellowtail = 1.1, and winter flounder = 0.6 (Murawski 1984). The 1979 distributions of standardized effort among fisheries and estimated catchability coefficients by species and fishery (Murawski 1984) are as follows:

Fishery	Standardized days fished	Estimated catchability coefficients ($\times 10^4$)			
		Cod	Haddock	Yellowtail	Winter flounder
1	2768 (14%)	0.24	0.18	0.70	0.26
2	2965 (15%)	0.10	0.21	1.55	0.25
3	593 (3%)	0.16	0.12	0.43	1.06
4	8105 (41%)	0.41	0.46	0.34	0.36
5	2768 (14%)	0.27	0.90	0.34	0.25
6	2570 (13%)	0.34	1.00	0.15	0.14

For several species (i.e., yellowtail and winter flounder), catchability coefficients vary by approximately an order of magnitude among fisheries, while cod exhibits relatively less variability among fisheries.

Values $F_{0.1}$ and F_{max} (conditional on mesh size) for the four stocks are given in Table 1. Mortality rates during 1979 were substantially greater than conditional $F_{0.1}$ and F_{max} values for all the stocks and mesh sizes. Various LP runs were made assuming $F_{0.1}$ and F_{max} for the stocks (Table 1) as fishing mortality constraints, and minimization of total effort (Σf_j) as the objective (Table 2). Output from the LP included total effort at the optimum feasible level, as well as the amount of fishing effort allocated to each fishery (expressed as a percentage of the total). In all eight LP runs it is clear that $F_{0.1}$ and F_{max} levels could be achieved simultaneously for all four stocks with substantially less total effort than was exerted in 1979 (48–79% less effort, depending on mesh size and $F_{0.1}$ or F_{max} constraint). Associated with the overall effort reductions were substantial shifts in the relative distribution of effort among fisheries. In all eight LP runs, fisheries 1 and 6 were eliminated, while fisheries 3 and 5 were allocated proportionally more effort in the optimal solutions than in 1979.

The sensitivity of LP solutions to various fishing mortality constraints, as well as to the assumed values of catchability coefficients (q_{ij}), was examined in more detail to assess the robustness of the results (Tables 3 and 4). The first set of sensitivity runs examined the effects of varying F levels on each species individually, while holding F values on the other three species constant (Table 3). In these three analyses, fishing mortality constraints were (1) $F_{0.1}$, (2) F_{max} for a 140-mm mesh (current industry standard net), and (3) F values exhibited in 1979. For the $F_{0.1}$ runs, fishing mortality was varied from −0.15 to +0.15 of the computed value for each species, in increments of 0.05. Fishing mortality varied from −0.30 to +0.30 of computed values in the F_{max} and F_{1979} runs. In 32% (23/72) of these sensitivity runs the LP solution was not feasible, generally indicating that extremely high or low F values for a particular species could not be achieved while maintaining moderate F levels on the other species. Interestingly, most of the infeasible solutions (52%) were for Atlantic cod. More than any other species, cod was a ubiquitous component of the six fisheries, whereas the majority of landings of the other three species were derived from one or two of the fisheries (i.e. yellowtail in fishery 5, haddock in fisheries 5 and 6, winter flounder in fishery 3). The fact that extremely high or low mortality rates on cod could not be achieved while maintaining moderate mortality rates on the other species is indicative of the more general distribution of cod in the Georges Bank region, and that they are caught in quantity by all six of the defined otter trawl fisheries (Murawski et al. 1983). Conversely, of the remaining 11 infeasible solutions, four were due each to yellowtail and winter flounders and three were for haddock.

The other four sets of sensitivity analyses addressed the question of impacts on the optimal solution of misestimation of the catchability coefficient, q_{ij} (Table 4). For each species and fishery, the catachability coefficient was varied from −30 to +30% of the estimated 1979 values, in increments of 10%. These runs were made assuming that fishing mortality constraints were F_{max} values for a 140-mm mesh. In general, both the optimal total effort value and the percent allocation of effort among fisheries changed little with various q_{ij}'s. The exception was for fisheries 5 and 6, particularly for those simulations examing changes in cod and haddock q's (Tables 3 and 4). Fisheries 5 and 6 exhibit relatively high proportions of cod and haddock compared with other species, and q values for cod and haddock are roughly similar in the two fisheries. Thus, it is not surprising that changes in relative q's for cod and haddock

TABLE 3. Sensitivity of linear programming solutions for optimal fishing effort and proportional allocation among competing otter trawl fisheries on Georges Bank to incremental changes in fishing mortality constraints on four demersal fish species.

	Fishing mortality rate[a]					% allocation by fishery					
Species	COD	HAD	YT	WF	Optimum total effort[b]	1	2	3	4	5	6
Fishing mortality constraints based on $F_{0.1}$ values for 140-mm mesh											
Atlantic cod	0.00	0.25	0.23	0.23	SI						
	0.05	0.25	0.23	0.23	SI						
	0.10	0.25	0.23	0.23	4 511	0.0	11.7	31.5	4.4	52.4	0.0
	0.20	0.25	0.23	0.23	5 574	0.0	5.3	9.6	77.4	7.8	0.0
	0.25	0.25	0.23	0.23	SI						
	0.30	0.25	0.23	0.23	SI						
Haddock	0.15	0.10	0.23	0.23	SI						
	0.15	0.15	0.23	0.23	4 877	29.3	0.7	20.2	49.8	0.0	0.0
	0.15	0.20	0.23	0.23	4 804	0.0	10.0	20.3	58.3	11.5	0.0
	0.15	0.30	0.23	0.23	5 282	0.0	6.5	18.5	32.5	42.5	0.0
	0.15	0.35	0.23	0.23	5 520	0.0	5.0	17.7	21.2	56.1	0.0
	0.15	0.40	0.23	0.23	5 759	0.0	3.6	17.0	10.9	68.5	0.0
Yellowtail flounder	0.15	0.25	0.08	0.23	SI						
	0.15	0.25	0.13	0.23	SI						
	0.15	0.25	0.18	0.23	4 832	0.0	1.1	21.5	47.1	30.3	0.0
	0.15	0.25	0.28	0.23	5 254	0.0	14.7	17.4	42.6	25.4	0.0
	0.15	0.25	0.33	0.23	5 465	0.0	20.6	15.6	40.5	23.2	0.0
	0.15	0.25	0.38	0.23	5 675	0.0	26.2	13.9	38.7	21.2	0.0
Winter flounder	0.15	0.25	0.23	0.08	SI						
	0.15	0.25	0.23	0.13	4 503	0.0	17.4	0.0	55.8	6.2	20.7
	0.15	0.25	0.23	0.18	4 764	0.0	11.2	8.7	52.4	27.8	0.0
	0.15	0.25	0.23	0.28	5 321	0.0	5.5	29.0	37.9	27.7	0.0
	0.15	0.25	0.23	0.33	5 600	0.0	3.0	37.6	31.7	27.7	0.0
	0.15	0.25	0.23	0.38	5 879	0.0	0.9	45.4	26.1	27.7	0.0
Fishing mortality constraints based on F_{max} for 140-mm mesh											
Atlantic cod	0.00	0.56	0.36	0.39	SI						
	0.06	0.56	0.36	0.39	SI						
	0.16	0.56	0.36	0.39	SI						
	0.36	0.56	0.36	0.39	10 198	0.0	0.5	7.4	65.8	26.3	0.0
	0.46	0.56	0.36	0.39	SI						
	0.56	0.56	0.36	0.39	SI						
Haddock	0.26	0.26	0.36	0.39	SI						
	0.26	0.36	0.36	0.39	8 179	0.0	6.8	20.1	58.2	14.9	0.0
	0.26	0.46	0.36	0.39	8 656	0.0	4.9	19.0	42.5	33.7	0.0
	0.26	0.66	0.36	0.39	9 612	0.0	1.6	17.1	15.7	65.6	0.0
	0.26	0.76	0.36	0.39	10 090	0.0	0.2	16.3	4.2	79.3	0.0
	0.26	0.86	0.36	0.39	SI						
Yellowtail flounder	0.26	0.56	0.06	0.39	SI						
	0.26	0.56	0.16	0.39	SI						
	0.26	0.56	0.26	0.39	8 772	0.0	0.0	25.9	21.6	17.3	35.2
	0.26	0.56	0.46	0.39	9 556	0.0	10.5	15.9	26.7	46.9	0.0
	0.26	0.56	0.56	0.39	9 978	0.0	17.3	14.0	25.2	43.6	0.0
	0.26	0.56	0.66	0.39	10 400	0.0	23.4	12.2	23.8	40.6	0.0
Winter flounder	0.26	0.56	0.36	0.09	SI						
	0.26	0.56	0.36	0.19	8 092	0.0	16.0	0.0	32.8	4.7	46.6
	0.26	0.56	0.36	0.29	8 577	0.0	6.1	6.0	35.9	52.0	0.0
	0.26	0.56	0.36	0.49	9 692	0.0	0.5	28.6	21.8	49.1	0.0
	0.26	0.56	0.36	0.59	10 276	0.0	0.0	40.2	12.6	33.7	13.6
	0.26	0.56	0.36	0.69	10 867	0.0	0.0	50.9	3.7	16.7	28.7

TABLE 3. (*Concluded*)

Species	Fishing mortality rate[a]				Optimum total effort[b]	% allocation by fishery					
	COD	HAD	YT	WF		1	2	3	4	5	6
Fishing mortality constraints based on F values for 1979											
Atlantic cod	0.30	1.00	1.10	0.60	SI						
	0.40	1.00	1.10	0.60	17 018	0.0	24.5	10.9	13.3	51.3	0.0
	0.50	1.00	1.10	0.60	18 082	0.0	21.8	5.3	35.3	37.6	0.0
	0.70	1.00	1.10	0.60	22 259	40.3	4.0	0.0	34.9	0.0	20.8
	0.80	1.00	1.10	0.60	SI						
	0.90	1.00	1.10	0.60	SI						
Haddock	0.60	0.70	1.10	0.60	17 938	5.8	20.8	0.5	73.0	0.0	0.0
	0.60	0.80	1.10	0.60	18 190	0.0	21.9	0.4	69.6	8.1	0.0
	0.60	0.90	1.10	0.60	18 667	0.0	20.6	0.4	62.0	17.0	0.0
	0.60	1.10	1.10	0.60	19 623	0.0	18.2	0.4	47.9	33.5	0.0
	0.60	1.20	1.10	0.60	20 101	0.0	17.1	0.4	41.4	41.1	0.0
	0.60	1.30	1.10	0.60	20 579	0.0	16.1	0.4	35.2	48.4	0.0
Yellowtail flounder	0.60	1.00	0.80	0.60	17 880	0.0	8.7	2.5	59.4	29.4	0.0
	0.60	1.00	0.90	0.60	18 302	0.0	12.4	1.8	57.8	28.1	0.0
	0.60	1.00	1.00	0.60	18 724	0.0	16.0	1.1	56.3	26.7	0.0
	0.60	1.00	1.20	0.60	19 573	0.0	22.8	0.0	53.0	22.6	1.6
	0.60	1.00	1.30	0.60	20 010	0.0	26.4	0.0	50.7	17.4	5.4
	0.60	1.00	1.40	0.60	20 447	0.0	29.9	0.0	48.6	12.5	9.1
Winter flounder	0.60	1.00	1.10	0.30	SI						
	0.60	1.00	1.10	0.40	SI						
	0.60	1.00	1.10	0.50	20 469	39.4	9.3	0.0	21.2	0.0	30.0
	0.60	1.00	1.10	0.70	19 703	0.0	17.6	6.1	50.8	25.5	0.0
	0.60	1.00	1.10	0.80	20 261	0.0	15.9	11.5	47.0	25.6	0.0
	0.60	1.00	1.10	0.90	20 818	0.0	14.3	16.6	43.5	25.6	0.0

[a] Instantaneous fishing mortality rates simulated for COD (Atlantic cod), HAD (haddock), YT (Yellowtail flounder), and WF (winter flounder).

[b] Equivalent days fished by otter trawlers, standardized by vessel size class and fishing gear type; SI = solution infeasible.

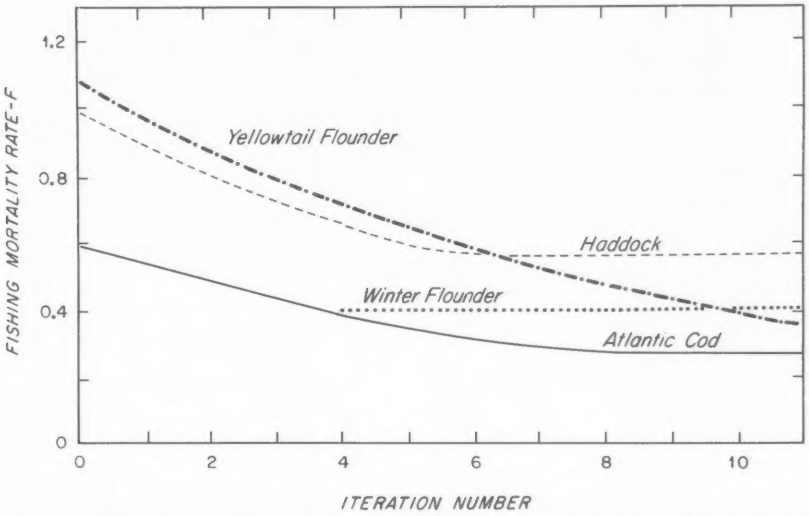

FIG. 1. Fishing mortality rate constraints on four Georges Bank fish stocks for sequential iterations of linear programming analyses determining optimal fishing effort distributions among six otter trawl fisheries.

TABLE 4. Sensitivity of linear programming solutions of optimal total fishing effort and proportional allocation among competing mixed-species otter trawl fisheries on Georges Bank to variations in catchability coefficients for each species and fishery (q). Fishing mortality constraints are F_{max} values for a 140-mm mesh.

	q ($\times 10^4$) by fishery						Optimal	% allocation by fishery					
Fishery	1	2	3	4	5	6	total effort[a]	1	2	3	4	5	6
							Atlantic cod						
1	0.17	0.10	0.16	0.41	0.27	0.34	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.19	0.10	0.16	0.41	0.27	0.34	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.22	0.10	0.16	0.41	0.27	0.34	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.26	0.10	0.16	0.41	0.27	0.34	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.29	0.10	0.16	0.41	0.27	0.34	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.31	0.10	0.16	0.41	0.27	0.34	9134	0.0	3.1	18.0	28.4	50.5	0.0
2	0.24	0.07	0.16	0.41	0.27	0.34	9143	0.0	3.1	17.9	28.8	50.2	0.0
	0.24	0.08	0.16	0.41	0.27	0.34	9140	0.0	3.1	17.9	28.6	50.3	0.0
	0.24	0.09	0.16	0.41	0.27	0.34	9137	0.0	3.1	18.0	28.5	50.4	0.0
	0.24	0.11	0.16	0.41	0.27	0.34	9131	0.0	3.1	18.0	28.3	50.6	0.0
	0.24	0.12	0.16	0.41	0.27	0.34	9128	0.0	3.2	18.0	28.2	50.6	0.0
	0.24	0.13	0.16	0.41	0.27	0.34	9125	0.0	3.2	18.1	28.0	50.7	0.0
3	0.24	0.10	0.11	0.41	0.27	0.34	9218	0.0	2.9	17.1	31.7	48.4	0.0
	0.24	0.10	0.13	0.41	0.27	0.34	9185	0.0	3.0	17.4	30.4	49.2	0.0
	0.24	0.10	0.14	0.41	0.27	0.34	9169	0.0	3.0	17.6	29.7	49.6	0.0
	0.24	0.10	0.18	0.41	0.27	0.34	9099	0.0	3.2	18.4	27.0	51.4	0.0
	0.24	0.10	0.19	0.41	0.27	0.34	9080	0.0	3.3	18.6	26.3	51.9	0.0
	0.24	0.10	0.21	0.41	0.27	0.34	9043	0.0	3.4	19.0	24.8	52.8	0.0
4	0.24	0.10	0.16	0.29	0.27	0.34	9636	0.0	7.3	19.5	35.1	0.0	38.1
	0.24	0.10	0.16	0.33	0.27	0.34	9418	0.0	8.6	22.7	25.6	0.0	43.2
	0.24	0.10	0.16	0.37	0.27	0.34	9266	0.0	2.8	16.5	33.5	47.2	0.0
	0.24	0.10	0.16	0.45	0.27	0.34	9039	0.0	3.4	19.1	24.7	52.9	0.0
	0.24	0.10	0.16	0.49	0.27	0.34	8968	0.0	3.6	19.9	21.8	54.8	0.0
	0.24	0.10	0.16	0.53	0.27	0.34	8913	0.0	3.8	20.5	19.5	56.3	0.0
5	0.24	0.10	0.16	0.41	0.19	0.34	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.24	0.10	0.16	0.41	0.22	0.34	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.24	0.10	0.16	0.41	0.24	0.34	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.24	0.10	0.16	0.41	0.30	0.34	8978	0.0	3.6	19.8	22.2	54.5	0.0
	0.24	0.10	0.16	0.41	0.32	0.34	8863	0.0	3.9	21.1	17.4	57.6	0.0
	0.24	0.10	0.16	0.41	0.35	0.34	8670	0.0	4.5	23.4	9.2	62.9	0.0
6	0.24	0.10	0.16	0.41	0.27	0.24	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.24	0.10	0.16	0.41	0.27	0.27	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.24	0.10	0.16	0.41	0.27	0.31	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.24	0.10	0.16	0.41	0.27	0.37	9075	0.0	10.7	27.9	9.8	0.0	51.6
	0.24	0.10	0.16	0.41	0.27	0.41	8863	0.0	11.9	31.0	0.0	1.7	55.4
	0.24	0.10	0.16	0.41	0.27	0.44	8787	0.0	10.6	30.1	0.0	14.0	45.3
							Haddock						
1	0.13	0.21	0.12	0.46	0.90	1.00	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.14	0.21	0.12	0.46	0.90	1.00	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.16	0.21	0.12	0.46	0.90	1.00	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.20	0.21	0.12	0.46	0.90	1.00	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.22	0.21	0.12	0.46	0.90	1.00	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.23	0.21	0.12	0.46	0.90	1.00	9134	0.0	3.1	18.0	28.4	50.5	0.0
2	0.18	0.15	0.12	0.46	0.90	1.00	9142	0.0	3.1	18.0	28.2	50.7	0.0
	0.18	0.17	0.12	0.46	0.90	1.00	9140	0.0	3.1	18.0	28.3	50.7	0.0
	0.18	0.19	0.12	0.46	0.90	1.00	9137	0.0	3.1	18.0	28.3	50.6	0.0
	0.18	0.23	0.12	0.46	0.90	1.00	9131	0.0	3.1	18.0	28.5	50.4	0.0
	0.18	0.25	0.12	0.46	0.90	1.00	9129	0.0	3.2	18.0	28.6	50.3	0.0
	0.18	0.27	0.12	0.46	0.90	1.00	9126	0.0	3.2	18.0	28.6	50.2	0.0

TABLE 4. (*Continued*)

Fishery	q ($\times 10^4$) by fishery						Optimal total effort[a]	% allocation by fishery					
	1	2	3	4	5	6		1	2	3	4	5	6
3	0.18	0.21	0.08	0.46	0.90	1.00	9166	0.0	3.0	17.9	27.5	51.5	0.0
	0.18	0.21	0.10	0.46	0.90	1.00	9150	0.0	3.1	18.0	28.0	51.0	0.0
	0.18	0.21	0.11	0.46	0.90	1.00	9142	0.0	3.1	18.0	28.2	50.7	0.0
	0.18	0.21	0.13	0.46	0.90	1.00	9126	0.0	3.2	18.0	28.6	50.2	0.0
	0.18	0.21	0.14	0.46	0.90	1.00	9118	0.0	3.2	18.0	28.8	50.0	0.0
	0.18	0.21	0.16	0.46	0.90	1.00	9103	0.0	3.2	18.0	29.3	49.4	0.0
4	0.18	0.21	0.12	0.32	0.90	1.00	9285	0.0	2.6	17.7	24.3	55.4	0.0
	0.18	0.21	0.12	0.37	0.90	1.00	9236	0.0	2.8	17.8	25.6	53.8	0.0
	0.18	0.21	0.12	0.41	0.90	1.00	9193	0.0	2.9	17.9	26.8	52.4	0.0
	0.18	0.21	0.12	0.51	0.90	1.00	9069	0.0	3.4	18.1	30.3	48.3	0.0
	0.18	0.21	0.12	0.55	0.90	1.00	9011	0.0	3.6	18.2	31.9	46.3	0.0
	0.18	0.21	0.12	0.60	0.90	1.00	8930	0.0	3.9	18.4	34.3	43.5	0.0
5	0.18	0.21	0.12	0.46	0.63	1.00	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.18	0.22	0.12	0.46	0.72	1.00	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.18	0.21	0.12	0.46	0.81	1.00	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.18	0.21	0.12	0.46	0.99	1.00	8962	0.0	3.7	18.3	33.3	44.6	0.0
	0.18	0.21	0.12	0.46	1.08	1.00	8831	0.0	4.2	18.6	37.2	40.0	0.0
	0.18	0.21	0.12	0.46	1.17	1.00	8726	0.0	4.6	18.8	40.3	36.2	0.0
6	0.18	0.21	0.12	0.46	0.90	0.70	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.18	0.21	0.12	0.46	0.90	0.80	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.18	0.21	0.12	0.46	0.90	0.90	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.18	0.21	0.12	0.46	0.90	1.10	9026	0.0	9.6	25.1	23.2	0.0	42.1
	0.18	0.21	0.12	0.46	0.90	1.20	8880	0.0	9.5	24.6	28.4	0.0	37.6
	0.18	0.21	0.12	0.46	0.90	1.30	8766	0.0	9.4	24.3	32.5	0.0	33.9
Yellowtail flounder													
1	0.49	1.55	0.43	0.34	0.34	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.56	1.55	0.43	0.34	0.34	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.63	1.55	0.43	0.34	0.34	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.77	1.55	0.43	0.34	0.34	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.84	1.55	0.43	0.34	0.34	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.91	1.55	0.43	0.34	0.34	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
2	0.70	1.09	0.43	0.34	0.34	0.15	9217	0.0	4.6	17.6	28.1	49.7	0.0
	0.70	1.24	0.43	0.34	0.34	0.15	9182	0.0	4.1	17.7	28.2	50.1	0.0
	0.70	1.40	0.43	0.34	0.34	0.15	9154	0.0	3.5	17.9	28.3	50.3	0.0
	0.70	1.71	0.43	0.34	0.34	0.15	9117	0.0	2.8	18.1	28.5	50.6	0.0
	0.70	1.86	0.43	0.34	0.34	0.15	9104	0.0	2.6	18.2	28.5	50.8	0.0
	0.70	2.02	0.43	0.34	0.34	0.15	9085	0.0	7.5	26.5	16.9	0.0	49.1
3	0.70	1.55	0.30	0.34	0.34	0.15	9223	0.0	4.7	17.5	28.0	49.7	0.0
	0.70	1.55	0.34	0.34	0.34	0.15	9196	0.0	4.3	17.7	28.1	49.9	0.0
	0.70	1.55	0.39	0.34	0.34	0.15	9162	0.0	3.6	17.9	28.3	50.2	0.0
	0.70	1.55	0.47	0.34	0.34	0.15	9106	0.0	2.6	18.1	28.5	50.7	0.0
	0.70	1.55	0.52	0.34	0.34	0.15	9071	0.0	2.0	18.3	28.7	51.0	0.0
	0.70	1.55	0.56	0.34	0.34	0.15	9043	0.0	1.4	18.5	28.8	51.3	0.0
4	0.70	1.55	0.43	0.24	0.34	0.15	9243	0.0	5.1	17.4	28.0	49.5	0.0
	0.70	1.55	0.43	0.27	0.34	0.15	9211	0.0	4.5	17.6	28.1	49.8	0.0
	0.70	1.55	0.43	0.31	0.34	0.15	9167	0.0	3.7	17.8	28.3	50.2	0.0
	0.70	1.55	0.43	0.37	0.34	0.15	9101	0.0	2.5	18.2	28.5	50.8	0.0
	0.70	1.55	0.43	0.41	0.34	0.15	9057	0.0	1.7	18.4	28.7	51.2	0.0
	0.70	1.55	0.43	0.41	0.34	0.15	9024	0.0	1.1	18.6	28.9	51.5	0.0
5	0.70	1.55	0.43	0.34	0.24	0.15	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.70	1.55	0.43	0.34	0.27	0.15	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.70	1.55	0.43	0.34	0.31	0.15	9192	0.0	4.2	17.7	28.2	50.0	0.0
	0.70	1.55	0.43	0.34	0.37	0.15	9076	0.0	2.1	18.3	28.7	51.0	0.0
	0.70	1.55	0.43	0.34	0.41	0.15	8997	0.0	0.6	18.7	29.0	51.7	0.0
	0.70	1.55	0.43	0.34	0.44	0.15	8952	0.0	0.0	19.4	28.6	49.5	2.5

TABLE 4. (*Concluded*)

Fishery	q ($\times 10^4$) by fishery						Optimal total effort[a]	% allocation by fishery					
	1	2	3	4	5	6		1	2	3	4	5	6
6	0.70	1.55	0.43	0.34	0.34	0.11	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.70	1.55	0.43	0.34	0.34	0.12	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.70	1.55	0.43	0.34	0.34	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.70	1.55	0.43	0.34	0.34	0.17	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.70	1.55	0.43	0.34	0.34	0.18	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.70	1.55	0.43	0.34	0.34	0.20	9126	0.0	8.2	26.2	16.8	0.0	48.8
							Winter flounder						
1	0.18	0.25	1.06	0.36	0.25	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.21	0.25	1.06	0.36	0.25	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.23	0.25	1.06	0.36	0.25	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.29	0.25	1.06	0.36	0.25	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.31	0.25	1.06	0.36	0.25	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.34	0.25	1.06	0.36	0.25	0.14	9134	0.0	3.1	18.0	28.4	50.5	0.0
2	0.26	0.18	1.06	0.36	0.25	0.14	9145	0.0	3.1	18.2	28.3	50.4	0.0
	0.26	0.20	1.06	0.36	0.25	0.14	9142	0.0	3.1	18.2	28.3	50.5	0.0
	0.26	0.23	1.06	0.36	0.25	0.14	9137	0.0	3.1	18.1	28.4	50.5	0.0
	0.26	0.28	1.06	0.36	0.25	0.14	9129	0.0	3.2	17.9	28.5	50.5	0.0
	0.26	0.30	1.06	0.36	0.25	0.14	9126	0.0	3.2	17.8	28.5	50.5	0.0
	0.26	0.33	1.06	0.36	0.25	0.14	9121	0.0	3.2	17.7	28.6	50.5	0.0
3	0.26	0.25	0.74	0.36	0.25	0.14	9593	0.0	0.9	26.8	22.9	49.4	0.0
	0.26	0.25	0.85	0.36	0.25	0.14	9386	0.0	1.9	22.9	25.3	49.9	0.0
	0.26	0.25	0.95	0.36	0.25	0.14	9249	0.0	2.6	20.3	27.0	50.2	0.0
	0.26	0.25	1.17	0.36	0.25	0.14	9045	0.0	3.6	16.2	29.5	50.7	0.0
	0.26	0.25	1.27	0.36	0.25	0.14	8979	0.0	3.9	14.8	30.4	50.9	0.0
	0.26	0.25	1.38	0.36	0.25	0.14	8910	0.0	11.5	19.4	20.4	0.0	48.7
4	0.26	0.25	1.06	0.25	0.25	0.14	9285	0.0	2.4	21.0	26.5	50.1	0.0
	0.26	0.25	1.06	0.29	0.25	0.14	9232	0.0	2.6	19.9	27.2	50.2	0.0
	0.26	0.25	1.06	0.32	0.25	0.14	9191	0.0	2.9	19.1	27.7	50.3	0.0
	0.26	0.25	1.06	0.40	0.25	0.14	9075	0.0	3.4	16.8	29.2	50.6	0.0
	0.26	0.25	1.06	0.43	0.25	0.14	9029	0.0	3.7	15.9	29.7	50.8	0.0
	0.26	0.25	1.06	0.47	0.25	0.14	8966	0.0	4.0	14.5	30.6	50.9	0.0
5	0.26	0.25	1.06	0.36	0.18	0.14	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.26	0.25	1.06	0.36	0.20	0.14	9219	0.0	9.8	25.6	16.6	0.0	48.0
	0.26	0.25	1.06	0.36	0.23	0.14	9186	0.0	2.9	19.0	27.8	50.3	0.0
	0.26	0.25	1.06	0.36	0.28	0.14	9057	0.0	3.5	16.4	29.4	50.7	0.0
	0.26	0.25	1.06	0.36	0.30	0.14	9007	0.0	3.8	15.4	30.0	50.8	0.0
	0.26	0.25	1.06	0.36	0.33	0.14	8931	0.0	4.2	13.8	31.0	51.0	0.0
6	0.26	0.25	1.06	0.36	0.25	0.10	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.26	0.25	1.06	0.36	0.25	0.11	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.26	0.25	1.06	0.36	0.25	0.13	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.26	0.25	1.06	0.36	0.25	0.15	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.26	0.25	1.06	0.36	0.25	0.17	9134	0.0	3.1	18.0	28.4	50.5	0.0
	0.26	0.25	1.06	0.36	0.25	0.18	9121	0.0	10.3	23.7	17.8	0.0	48.2

[a] Equivalent days fished by otter trawlers, standardized by vessel size class and fishing gear type.

among the two fisheries can substantially alter the allocation of effort among them.

Results of these analyses indicate that $F_{0.1}$ or $F_{\max}$ values could be achieved for all species simultaneously by substantially reducing total fishing effort from 1979 levels, and by allocating the remaining effort among the six fisheries in a much different pattern.

The greatest proportional changes in fishing mortality rates were due to the overall reduction in effort. Smaller changes in F's were attributable in this example to the effort reallocation procedure. When overall effort was reduced to 9134 standardized days and the 1979 effort allocation pattern was retained, the resulting F values for cod, haddock, yellowtail, and winter flounder were 0.28, 0.46, 0.50, and 0.28, respectively. The "optimal" effort pattern associated with $F_{\max}$ for a 140-mm mesh resulted in F values of 0.26, 0.56, 0.36, and 0.39 for the four stocks. Thus, both effort reduction and reallocation were important in achieving fishing mortality rate goals for all stocks simultaneously.

The implementation of results of the analyses could result in severe negative economic and social impacts in the short term. As previously described, the "optimal" effort solution could be implemented over a number of fishing seasons to lessen the impacts of effort reduction and reallocation. Accordingly, this strategy was simulated by incrementally reducing F constraints on the four species from 1979 values to $F_{\max}$ levels over a number of time steps (Fig. 1 and 2). Fishing mortality constraints were reduced 10% per iteration (year) from 1979 levels, until the $F_{\max}$ level for a 140-mm-mesh net for the species was achieved (Fig. 1). At each iteration the LP model was rerun with the new F constraints for each species. Figure 2 illustrates the impacts of incremental reductions in F's on the total amount of effort and allocation among the six fisheries. The $F_{\max}$ values for all species were achieved in 11 interations under this strategy. Initially, fishery 4 was allocated most of the effort; however, as $F_{\max}$ levels on winter flounder and haddock were achieved, the amount of effort in fishery 4 declined, with concomitant increases in fisheries 3 and 5. Fisheries 1 and 6 were not allocated any effort in these analyses.

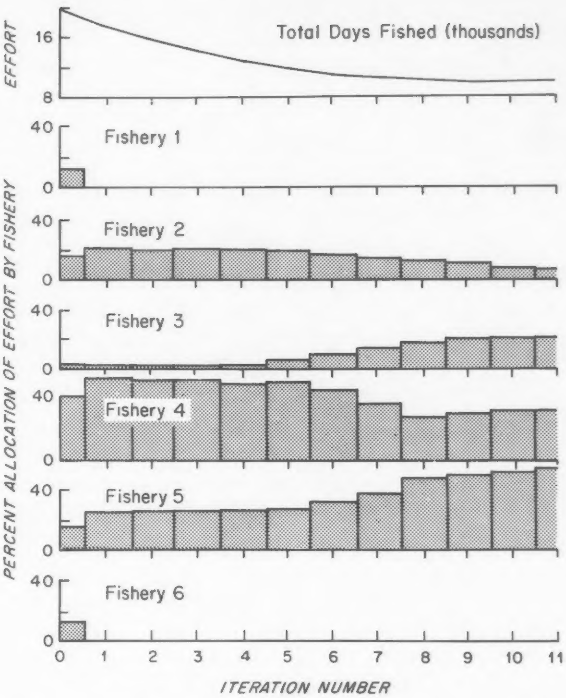

FIG. 2. Linear programming solutions of optimal total fishing effort (standardized days fished) and proportional allocation among six otter trawl fisheries in the Georges Bank region. The total effort value and distribution among fisheries at iteration 0 is equivalent to values exhibited during 1979. At each succeeding iteration, effort is constrained such that fishing mortality rates specified in Fig. 1 are maintained with a minimum of total effort.

Discussion

LP models described and illustrated herein make use of the additivity of instantaneous mortality rates (among fisheries) and the assumed linear relationship between fishing effort and fishing mortality. Although the linearity assumption is critical to the proposed model formulation, the problem may be recast by dividing the relationship into a series of piece-wise linear segments, or by using other mathematical programming techniques, if the functional relationship between f and F is nonlinear.

Shepherd and Garrod (1982) have criticized the use of LP models for these types of fishery allocation problems on the basis that the LP formulation may not be sufficiently defined to account for the substantial inertia that would characterize actual allocation problems ("...the LP method inherently leads to solutions that are extreme, sparse, and ruthless"). They noted that the LP solutions are often quite different from initial conditions even though the advantages of the solution are small, the LP solutions may be sensitive to small variations in model coefficients, and the LP solutions generally utilize only a small number of potential alternatives (in this context only a small number of possible fisheries). However, as they pointed out, these characteristics of the LP method may be ameliorated by adding constraints to the model and reformulating the problem. For example, to reduce the "ruthless" behavior of the solution, constraints may be formulated specifying that particular LP solutions may not vary more than a fixed percentage from initial conditions in terms of resource allocation among activities, and that the LP solution cannot eliminate several of the optional activities. If the objectives of the reallocation scheme represent a considerable change from current conditions (e.g. present fishing mortality rates are substantially greater than F objectives for the species), then in order to reduce F levels gradually the LP solution could be implemented over a number of time steps during which F levels are reduced sequentially (Fig. 1 and 2). The LP model can thus be specified with sufficient additional constraints to account for the initial state of the fishery system and the potential adverse consequences of implementing an LP solution based solely on F objectives. Socioeconomic factors affecting the allocation scheme can be accounted for by modifying the objective function as well. However, the complexity of the model formulation increases substantially as these factors are considered (e.g. gross and net revenue versus the relative costs of operation in particular fisheries).

Resulting outputs of these LP analyses are optimal total effort levels and allocations among component fisheries, under fishing mortality constraints for each species. If recruitment is invariant over time for all stocks, then the expected total landings and species composition from each fishery would not change. However, given that recruitment to each stock is likely to vary widely, then landings in each fishery will also change if F levels are maintained at constant levels. Considerable variation in landings among the fisheries is likely, since recruitment to the various stocks is generally asynchronous (Sissenwine et al. 1982). If recruitment of a particular species is high relative to the others, then there may be substantial incentive for operators to transfer effort from those fisheries that take little of the abundant species (low q_{ij}) to those fisheries where the species is taken in quantity. The result of such a situation would be to increase mortality differentially on the abundant species. This would defeat the purpose of the allocation scheme, which is to maintain F levels on all the stocks, irrespective of the absolute catch level.

Catch optimization strategies for multispecies fisheries have been criticized on the basis of the volatile nature of by-catch ratios which are a principal component of the analysis. Similarly, effort optimization strategies are sensitive to interannual variation in catchability coefficients. Obviously, for fisheries that are prosecuted during a relatively short season or that involve highly migratory species, variability in catchability coefficients between fishing seasons may be too great to employ effort allocation methods with reasonable expectations that mortality rate objectives will be approximated. However, for many situations (e.g some groundfish fisheries), effort allocation procedures appear feasible, particularly since adjustments in effort could be made partway through the fishing season if species catchabilities appear to differ significantly from those predicted.

We have proposed objective methods for assessing the feasibility of simultaneous fishing mortality goals for a series of species, based on manipulating the spatial/temporal pattern of mixed-species harvests. A logical next step is to evaluate the effects of candidate strategies identified by LP on aggregate yields by species and fishery. Mixed-species yield analyses in both equilibrium (Murawski 1984) and dynamic (Overholtz and Murawski 1985) modes have been developed for such purposes. When used in conjunction with the LP results, these yield models allow an integrated approach to identification of feasible harvesting scenarios, and assessment of their impacts on yields to the fisheries and the abundance and age structure of the populations.

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Bounds on the Optimal Age-at-First-Capture for Stochastic, Age-Structured Fisheries[1]

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Lovejoy, W. S. 1986. Bounds on the optimal age-at-first-capture for stochastic, age-structured fisheries. Can. J. Fish. Aquat. Sci. 43: 101−107.

This paper addresses the problem of optimally exploiting an age-structured fishery with stochastic, density-dependent recruitment; stochastic dynamics; and cohort-dependent prices, costs, catchabilities, and survival rates. Sufficient conditions are derived for an age-at-first-capture to be a necessary component of the optimal management regime, and a lower bound on this critical age is calculated. The method consists of replacing the stochastic, density-dependent model with more traditional (stochastic, density-independent and deterministic, density-independent) models which yield lower bounds on the optimal escapement. A numerical example demonstrates the practical applicability of the results.

La présente communication traite du problème de l'exploitation optimale de stocks structurés par âges à recrutement stochastique dépendant de la densité et à dynamique stochastique et où les prix, les coûts, les potentiels de capture et les taux de survie sont fonction des cohortes. L'auteur obtient les conditions nécessaires à l'utilisation de l'âge à la première capture comme paramètre du régime de gestion optimale et calcule une limite inférieure pour cet âge critique. La méthode consiste à remplacer le modèle stochastique dépendant de la densité par des modèles plus classiques (stochastiques, indépendants de la densité et déterministes, indépendants de la densité) permettant d'obtenir des limites inférieures pour l'échappée optimale. L'application pratique des résultats est démontrée par un exemple numérique.

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In fishery management models, age-dependent attributes such as size, weight, value, and reproductive capacity can significantly affect optimal harvesting policies. These effects can be obscured by aggregating all age-classes into one lumped parameter, as is common in practice. The deficiencies of these "lumped parameter" models are well known (cf. Clark 1976; Mendelssohn 1978); only their simplicity recommends them over age-structured models. An age-structured model with n age-classes, or "cohorts," would require an n-dimensional vector, rather than a single real variable, to represent the state of the system (e.g. population or biomass level). This increased dimensionality greatly complicates both analytical and numerical calculations. For this reason the age-structured, or multi-cohort, fishery problem has been approached with a variety of simplifying assumptions.

Clark et al. (1973) solved the problem of the optimal exploitation of a cohort as it moves through time, assuming deterministic dynamics and constant catchability coefficients, costs, and survival rates. If recruitment is constant and cohorts can be selectively harvested, then in a multi-cohort fishery each cohort may be treated independently to achieve the optimal harvesting policy. The main result is the derivation of a "Fisher rule," which requires abstention from harvesting until a cohort reaches some age t^*, called the age-at-first-capture. This result derives from the assumption of rapid growth rates early in life. Harvesting is foregone as long as fish in the water grow in value at a rate faster than they dissipate due to time discounting and natural mortality.

Beddington and Taylor (1973) employed a Leslie matrix to incorporate age structure in their population model. This approach can incorporate age-dependent survival rates and recruitment as a linear function of the state vector. However, restricting the dynamics to this linear format may not yield ecologically interesting solutions (Mendelssohn 1976).

Stochastic multi-cohort models adopt another level of complexity. Spulber (1985) presented some existence results for optimal policies for the stochastic multi-cohort problem, and partially characterized the optimal policy for the problem with linear returns to harvest. Mendelssohn (1978) completely characterized the optimal policy, a modified Fisher rule, for the stochastic problem with linear returns to harvest and density-independent recruitment, and provided sufficient conditions for this policy format to extend to the density-dependent case.

The authors who succeeded in characterizing optimal policies (i.e. Clark et al. 1973; Mendelssohn 1978) recommended an age-at-first-capture as a necessary part of the management regime. However, a number of the assumptions they imposed will be challenged by real-world fisheries, and it is of interest whether an age-at-first-capture is appropriate for these more complicated systems. Specifically, an actual fishery system will have some or all of the following attributes.

(1) Recruitment will be density-dependent, i.e. will depend upon stock size, but it is likely that no empirically justifiable stock−recruitment relationship will exist.

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[1] This is a revised version of Chapter 5 of the author's Ph.D. dissertation at the University of Delaware.

(2) Subject as they are to environmental perturbations, recruitment and natural mortality will be random variables. However, it is likely that the relevant distributions will be unknown.

(3) Cohorts, or age-classes, may be separated in space, as in migrating species. For example, shrimp in the Gulf of Mexico move offshore as they grow (Blomo et al. 1982). Thus, larger shrimp are more sparse and require longer travel times to harvest than smaller shrimp. Under these conditions, catchability coefficients and the cost of producing effort can vary from one cohort to the next.

(4) Stock density will affect ease of capture, generating returns for harvest that depend nonlinearly on stock size.

(5) The ex-vessel price for individuals of a given cohort may depend upon the harvest of individuals in other cohorts (there may exist cross-elasticities of demand between cohorts).

(6) Effort directed at one cohort will extract individuals from other cohorts as incidental by-catch.

This paper incorporates the first four of the above attributes into a general model that includes the models of Clark et al. (1973) and Mendelssohn (1978) as special cases. Conditions are derived under which an age-at-first-capture will be a necessary component of the optimal management policy, and a lower bound on this critical age is calculated. The method consists of replacing the stochastic, density-dependent model with more traditional models (Stochastic, density-independent and deterministic, density-independent) which yield lower bounds on the optimal escapement. A numerical example demonstrates the practical applicability of the results.

The model retains the assumptions of constant price and perfectly discriminating gear, i.e. the price of fish is constant for each cohort (although it can vary from one cohort to another) and effort directed at a cohort will capture fish from that cohort only. The validity of the constant price assumption is suspect in many fisheries, and the model below must be considered an approximation in this regard. The quality of the approximation will depend upon the specific fishery in question. The assumption of perfectly discriminating gear is likewise an approximation to reality, but not unreasonable for fisheries in which cohorts are spatially segregated. For example, in the Atlantic surf clam fishery, clam beds seem to be dominated by a single cohort. Synchronous spawning in a clam bed will generate a platoon of planktonic larvae that, subject to the same currents and eddies, may well settle out together to form a new bed. Harvesters, then, can discriminate cohorts by discriminating clam beds. Migratory species may also exhibit spatially segregated cohorts. Shrimp in the Gulf of Mexico have already been mentioned in this regard.

The Model

Assume a fishery system with n cohorts, or age-classes, and let:

$x_i(t)$ = stock size (number of individuals) in cohort i at the beginning of time period t. Let $x(t) \in R^n$ denote the population vector with components $x_i(t)$. For each cohort i, we assume that $m_i \leq x_i(t) \leq M_i$ for all t, for some real numbers m_i and M_i satisfying $0 < m_i \leq M_i$. An appropriate choice of m_i and M_i can contain all relevant solutions. Indeed, harvesting the last fish in any cohort will be infinitely costly (see equation 4 below with zero escapement), so sufficiently small $m_i > 0$ will not exclude any interesting solutions. M_i may be arbitrarily large. Let $S = \{x \in R^n : m_i \leq x_i \leq M_i, i = 1 \text{ to } n\}$ denote the set of all possible states.

$y_i(t)$ = escapement (number of individuals) in cohort i at the end of period t. For any i we must have $m_i \leq y_i(t) \leq x_i(t)$. We assume that biological factors such as spawning and natural mortality are incorporated into the transfer function between time periods (see below), so that during the time period the fish stock is only altered via harvesting activity. Thus, the harvest of cohort i during period t will be $x_i(t) - y_i(t)$ individuals. It is mathematically convenient to use escapement, rather than harvest, as our control variable.

Throughout this paper I will be dealing with monotonicity issues involving vectors. If x and x' are in R^n, we define $x \geq x'$ to mean $x_i \geq x_i'$ for all components $i = 1$ to n. Likewise, given two vector-valued functions δ and δ' defined on a set S, we say $\delta \geq \delta'$ if $\delta(x) \geq \delta'(x)$ for all $x \in S$. The notation $V \circ g$ will be used to denote composite functions, i.e. $V \circ g(x) = V(g(x))$. For any real numbers a and b, we define $(a \wedge b) = \min \{a,b\}$.

The problem is modelled as a sequential decision process. A discrete-time model is used because in actual fisheries the controls (management plans) are typically adopted on a periodic (e.g. annual) basis. At each discrete time $t = 0,1,2,\ldots$ we observe the state of the system, $x(t)$, and choose an escapement, $y(t)$. As a result of these actions two things occur: (1) we immediately receive a reward $r(x(t),y(t))$, where r is a real valued function of the state and escapement, and (2) the system transfers to the next time period with initial stock

(1) $x(t + 1) = g(y(t),d(t))$

where g is a vector-valued function giving us the stock at time $t + 1$ as a function of the escapement in period t and a random vector $d(t)$ taking values on a convex sample space D. At each time period, t, the random disturbance, $d(t)$, is generated from a generic, stationary probability distribution. The transfer function g is assumed to be of the form

(2) $g(y,d) = (f(y,d_0), d_1y_1, d_2y_2, \ldots, d_{n-1}y_{n-1})$

where $f(y,d_0)$ is the recruitment to the first cohort due to spawning activity and is a function of the entire escapement vector y and the random variable d_0; f is assumed continuous and nondecreasing in y for fixed d_0 and Borel-measurable in d_0.

These assumptions are satisfied by most common recruitment functions appearing in the literature. For any y we must have $m_1 \leq f \leq M_1$ with probability one. The d_i for $i = 1$ to $n - 1$ are random survival rates. If $y_i(t)$ fish are left in cohort i at the end of period t, then $x_{i+1}(t + 1) = d_i(t)y_i(t)$ will survive to enter cohort $i + 1$ at the beginning of period $t + 1$. Thus, we must have $(m_{i+1}/m_i) \leq d_i \leq 1$ with probability one. Again, since the m_i's can be chosen as arbitrarily small positive numbers, this is a technical rather than practical restriction on the model. Individuals left in cohort n at the end of each time period are assumed to be lost to the system.

Returns in period t will be discounted by a factor α^t, where $\alpha \in [0,1)$. Our objective is to sequentially observe x and choose y so as to maximize the expected sum of the discounted returns over an infinite planning horizon. Define the feasible control set for state x, $\Omega(x) = \{y : m_i \leq y_i \leq x_i \text{ for all } i\}$. A policy is a (Borel) function $\delta(x)$ that associates with each state

x an escapement $y = \delta(x) \in \Omega(x)$. That is, given any state vector x, a policy tells us which escapement vector in $\Omega(x)$ to choose. We seek a policy that attains the maximum in

$$(3) \quad \max E \sum_{t=0}^{\infty} \alpha^t r(x(t), \delta(x(t)))$$

where $x(t + 1) = g(\delta(x(t)), d(t))$ and E denotes the expected value of the infinite sum.

We wish the solution of problem (3) to reflect a social optimum, i.e. to maximize the value to society of harvesting activity over an infinite time horizon. To this end, the appropriate return function r for harvesting a fishery resource from x to y in one time period will include the consumption benefits for consuming the harvest (x-y), less the opportunity cost of resources directed toward the procurement of that harvest. Define

p_i = ex-vessel price ($) for one individual from cohort i
c_i = cost ($) of generating one unit of effort directed at cohort i
q_i = catchability coefficient for cohort i normalized so that time periods have unit length

With the assumptions of constant price and selective harvesting of cohorts, the net social benefit for harvesting the population from x down to y in one time period is

$$(4) \quad r(x,y) = \sum_{i=1}^{n} r_i(x_i,y_i) = \sum_{i=1}^{n} p_i(x_i - y_i) - (c_i/q_i) \ln (x_i/y_i).$$

A complete statement of the above multi-cohort fishery problem is to find an escapement policy δ^* that maximizes (3) where r is given by (4), g is given by (2), and d is a random vector generated independently each time period according to a generic probability distribution. Let $V^*(x)$ denote the optimal value function starting in state $x \in S$, i.e. the maximum possible expected discounted value to society (eq. 3) that can be achieved starting at time zero in state x. The V^* is achieved by following an optimal policy δ^*. We will call this problem P. Problem P is a Markov decision process and can theoretically be solved by a successive approximations algorithm (cf. Heyman and Sobel 1984). Numerically, however, this problem is intractable for even modest n. Consider, for example, a discretized population with 10 cohorts and 100 population levels per cohort. The resulting program would have 10^{20} states requiring some 10^{60} calculations per iteration of successive approximations, exceeding the capabilities of existing computers.

We can, however, use the results in Lovejoy (1983) to construct approximate problems, easier to solve, that generate informative bounds on the optimal policy to problem P. This is pursued in the following section.

Results and Policy Bounds

Before moving to more specific models, I present the following general result.

Lemma 1: $V^*(x)$ is continuous and nondecreasing on S.
Proof: The proof is by induction, and utilizes known results for solving Markov decision processes by successive approximations (cf. Heyman and Sobel 1984). For any $x \in S$ and $V_k \in B(S)$ = {bounded, real-valued Borel functions on S}, define

$$(5) \quad V_{k+1}(x) = \max \{r(x,y) + \alpha E V_k \circ g(y,d) : y \in \Omega(x)\}.$$

Assume inductively that V_k is continuous and nondecreasing on S, then the maximum in equation (5) is attained and V_{k+1} will be continuous on S. To show that V_{k+1} is nondecreasing, consider any $x \geq x'$ in S. Let $\delta_{k+1}(x')$ attain the maximum in equation (5) for state x', and let $y = \delta_{k+1}(x') + (x - x') \geq \delta_{k+1}(x')$. It can readily be verified that $y \in \Omega(x)$ and $r(x', \delta_{k+1}(x')) \leq r(x,y)$. Hence, since g is nondecreasing in y and V_k is assumed nondecreasing on S:

$$\begin{aligned} V_{k+1}(x') &= r(x', \delta_{k+1}(x')) + \alpha E V_k \circ g(\delta_{k+1}(x'), d) \\ &\leq r(x,y) + \alpha E V_k \circ g(y,d) \leq V_{k+1}(x). \end{aligned}$$

Hence, V_{k+1} is nondecreasing on S. The induction can be initiated with any V_0 continuous and nondecreasing on S, and it is known that the sequence $\{V_k\}$ will converge uniformly to V^*. Hence, V^* will be continuous and nondecreasing on S.

Lemma 1 states, essentially, that you cannot be worse off by starting with more fish. This result is intuitively clear. As a consequence of Lemma 1, fish allowed to escape capture will never hurt future returns, because $V^* \circ g(y,d)$ will be nondecreasing in y. This, too, is intuitively sound; a fish left in the water can grow and spawn, and future returns will never suffer for these activities. We cannot solve for V^* due to the unacceptable calculational burden of doing so. However, suppose we approximate the problem by replacing f, the recruitment function, with R, a constant satisfying $m_1 \leq R \leq M_1$, i.e. let

$$g'(y,d) = (R, d_1 y_1, d_2 y_2, \ldots, d_{n-1} y_{n-1})$$

and let problem P' denote problem P with g' replacing g. Define δ'^* and V'^* for problem P' analogously to δ^* and V^* for problem P. Using the same reasoning as Lemma 1, V'^* will be continuous and nondecreasing on S.

The following proposition is worded in a manner that allows for nonunique optima in problems P, P', or both. Essentially, the proposition states that an optimal policy for problem P' is a rigorous lower bound for an optimal policy for problem P.

Proposition 1: For all x in S, for all $\delta'^*(x)$ there exists a $\delta^*(x) \geq \delta'^*(x)$, and for all $\delta^*(x)$ there exists a $\delta'^*(x) \leq \delta^*(x)$.
Proof: It can be verified that problem P' is separable into n subproblems (cf. Lovejoy 1983) and hence, $V'^* = \sum_{i=1}^{n} v_i'^*$, i.e. the optimal value function for problem P' is separable by cohort. Let

$$h(x,y,V) = r(x,y) + \alpha E V \circ g(y,d) \qquad x \in S,\ y \in \Omega(x),\ V \in B(S)$$

$$h'(x,y,V) = r(x,y) + \alpha E V \circ g'(y,d) \qquad x \in S,\ y \in \Omega(x),\ V \in B(S).$$

For any $x \in S$, $y \geq y'$, and any vector d, note that since V'^* is nondecreasing on S:

$$\begin{aligned} V'^* \circ g(y,d) - V'^* \circ g(y',d) &= v_1'^*(f(y,d)) \\ &\quad - v_1'^*(f(y',d)) + \sum_{i=2}^{n} v_i'^*(d_{i-1} y_{i-1}) \\ &\quad - v_i'^*(d_{i-1} y'_{i-1}) \geq \sum_{i=2}^{n} v_i'^*(d_{i-1} y_{i-1}) \\ &\quad - v_i'^*(d_{i-1} y'_{i-1}) = V'^* \circ g'(y,d) - V'^* \circ g'(y',d). \end{aligned}$$

Hence, for any $x \geq x'$ in S and any $y \in \Omega(x)$, $y' \in \Omega(x')$ with $y \geq y'$:

$$h(x,y,V'^*) - h(x',y',V'^*) \geq h'(x,y,V'^*) - h'(x',y',V'^*).$$

The result now follows from Lovejoy (1983) Proposition 3.8.

This is not surprising from an economic perspective. By approximating f with R we are removing any relationship between escapement at time t and recruitment to the first cohort at time $t + 1$. The essence of fisheries management is to strike a balance between the value of fish on the dock and the expected returns for leaving fish in the water. These future returns are due to the potential capture of the fish after a period of growth, as well as the contribution of fish in the water to future value via spawning activity. By replacing $f(y,d)$ with R, we are neglecting the marginal contribution of fish in the water to spawning, and are effectively decreasing the value of fish in the water relative to fish on the dock. Hence, the approximate problem P' will call for increased harvests (decreased escapements) relative to the original problem P.

Problem P' is not nearly as burdensome computationally as problem P. Indeed, problem P' is separable in that it can be solved in a decomposed manner as n smaller subproblems (see Lovejoy 1983 for details). This tractability is the primary reason a density-independent stock−recruitment relation is so often invoked in the literature. Proposition 1 states that an optimal policy for the tractable problem P' provides a lower bound for an optimal policy for the intractable problem P.

Suppose, for example, that starting in state x, the optimal escapement in problem P' for some cohort i satisfies $\delta_i'^*(x) = x_i$, i.e. we do not harvest any individuals from cohort i. From Proposition 1 we know

$$x_i = \delta_i'^*(x) \leq \delta_i^*(x) \leq x_i$$

where the last inequality is from the constraint set $\Omega(x)$. Thus, equality prevails throughout and we have $\delta_i^*(x) = x_i$, i.e. an optimal policy in problem P will call for abstention from harvesting cohort i. Mendelssohn (1978, Theorem 3a) said essentially the same thing: if we choose not to harvest neglecting spawning activity then we certainly will not harvest if we consider spawning activity.

As a second approximation, let θ = expected value of d, and define

$$g''(y) = (R, \theta_1 y_1, \theta_2 y_2, \ldots, \theta_{n-1} y_{n-1}).$$

Let P'' denote the fishery problem with g'' replacing g, and define V''^* and δ''^* for problem P'' analogously to V^* and δ^* for problem P.

Problem P'' is a deterministic problem with density-independent recruitment, and as such is only a slight generalization (to the case with cohort-dependent costs, survival rates, and catchabilities) of the problem analyzed by Clark et al. (1973). In that paper the optimal policy depends upon the growth rate of the value of an individual relative to the constant rate of dissipation due to time discounting and natural mortality. If an individual grows in value rapidly at an early age, only to tape off or even decrease in value later in life, Clark et al. (1973) concluded that we should abstain from harvesting up to a critical age, and then harvest at some positive level until potential profits are exhausted. The simplicity of the model contributes greatly to its transparency and intuitive appeal. The extension to cohort-dependent costs, catchabilities, and survival rates presents some additional complications. Not only does the value of fish vary with time, but so do their availability, cost of capture, and mortality rate. Some order can be imposed by assuming that

$$c_i/q_i \geq \alpha c_{i+1}/q_{i+1}.$$

The c/q ratio is a measure of the cost of capture of fish. A high c/q ratio indicates low availability of fish and high cost of fishing activity. A typical scenario may have c/q decreasing early in life and increasing later in life. The above assumption indicates that c/q cannot increase at a rate higher than the discount rate. Thus, if we were to consider only harvesting costs, we would tend to leave fish in the water, capturing them at some future time. I will return to this topic later.

The assumption that p_i enjoys a dramatic increase early in life only to level off or even decrease later is maintained. This is a reasonable scenario, if only because the physical growth rate of an individual usually follows such a pattern. The proposition below gives the form that δ''^* will take under these circumstances.

Define $\bar{x}_i = c_i/(q_i p_i)$. Then $\bar{x}_i$ is the solution to max $\{r_i(x_i,y_i) : y_i \text{ unrestricted}\}$, and represents the escapement at which the price of fish just equals the marginal harvesting cost for cohort i.

Proposition 2: Assume in problem P'' that for all cohorts i, $c_i/q_i \geq \alpha c_{i+1}/q_{i+1}$. If there exist cohorts i_1 and i_2, possibly equal, such that

$$\begin{aligned} &p_i \leq \alpha\theta_i p_{i+1} && i \leq i_1 \\ &\alpha\theta_i p_{i+1} \leq p_i \leq \theta_i \frac{c_i/q_i}{c_{i+1}/q_{i+1}} p_{i+1} && i_1 < i \leq i_2 \\ &p_i \geq \theta_i \frac{c_i/q_i}{c_{i+1}/q_{i+1}} p_{i+1} && i > i_2 \end{aligned}$$

then an optimal policy will satisfy

$$\begin{aligned} &\delta_i''^*(x) = x_i && i \leq i_1 \\ &\delta_i''^*(x) \quad \begin{cases} = x_i \text{ if } x_i \leq \bar{x}_i \\ \in [\bar{x}_i, x_i] \text{ otherwise} \end{cases} && i_1 < i \leq i_2 \\ &\delta_i''^*(x) = (x_i \wedge \bar{x}_i) && i > i_2. \end{aligned}$$

Proof: With $f(y,d_0) = R$, the problem satisfies the separability assumptions in Lovejoy (1983) and can be solved in a decomposed manner for

$$V''^*(x) = \sum_{i=1}^{n} v_i''^*(x_i) \text{ and } \delta''^*(x) = \mathop{X}_{i=1}^{n} \delta_i''^*(x_i)$$

using the recursion

$$(6) \quad v_i''^*(x_i) = \max \{r_i(x_i,y_i) + \alpha v_{i+1}''^*(\theta_i y_i)\}$$

where the maximum is taken over $y_i \in [m_i, x_i]$ and

$$r_i(x_i,y_i) = p_i(x_i - y_i) - (c_i/q_i)\ln(x_i/y_i).$$

$\delta_i''^*(x_i)$ will equal a maximizing argument y_i in equation (6).

It can readily be verified that for fixed x_i, r_i is concave in y_i with a global unconstrained maximum at $y_i = \bar{x}_i$. Hence, since $v_i''^*$ is nondecreasing in x_i, $J_i(x_i,y_i) = r_i(x_i,y_i) + \alpha v_{i+1}''^*(\theta_i y_i)$ will be nondecreasing in y_i up to $\bar{x}_i$, and perhaps further. Recall that m_i is chosen small enough so that it is nonbinding. Thus, for all cohorts i, $\delta_i''^*(x_i) = x_i$ if $x_i \leq \bar{x}_i$ and

$\delta_i''^*(x_i) \in [\bar{x}_i, x_i]$ if $x_i > \bar{x}_i$. To prove the result for $i > i_2$, we have for cohort n (where there is no future)

$$\delta_n''^*(x_n) = \begin{cases} x_n & \text{if } x_n \le \bar{x}_n \\ \bar{x}_n & \text{if } x_n > \bar{x}_n \end{cases}$$

and hence

$$v_n''^*(x_n) = \begin{cases} 0 & \text{if } x_n \le \bar{x}_n \\ p_n(x_n - \bar{x}_n) - (c_n/q_n)\ln(x_n/\bar{x}_n) & \text{if } x_n > \bar{x}_n. \end{cases}$$

Assume inductively that cohort $i + 1$ has an optimal policy and value function as stated for cohort n. Then

$$J_i(x_i,y_i) = p_i(x_i - y_i) - (c_i/q_i)\ln(x_i/y_i) + \alpha \begin{cases} 0 & \text{if } \theta_i y_i \le \bar{x}_{i+1} \\ p_{i+1}(\theta_i y_i - \bar{x}_{i+1}) - (c_{i+1}/q_{i+1})\ln(\theta_i y_i/\bar{x}_{i+1}) \end{cases}$$

otherwise.
If $\theta_i y_i > \bar{x}_{i+1}$ then

$$\begin{aligned} \partial J_i/\partial y_i &= -p_i + \alpha\theta_i p_{i+1} + (1/y_i)(c_i/q_i \\ &\quad - \alpha c_{i+1}/q_{i+1}) \le -p_i + \alpha\theta_i p_{i+1} + ((\theta_i/\bar{x}_{i+1})(c_i/q_i \\ &\quad - \alpha c_{i+1}/q_{i+1}) = -p_i + \theta_i p_{i+1}(c_i/q_i)/(c_{i+1}/q_{i+1}) \\ &\le 0 \text{ by assumption for } i > i_2. \end{aligned}$$

Hence, a maximizing y_i will satisfy $\theta_i y_i \le \bar{x}_{i+1}$ implying $v_{i+1}''^*(\theta_i y_i) = 0$ and the optimal policy is as stated. The induction can be initiated with $v_n''^*$ and the result is proved for $i > i_2$.

The stated attributes for $i_1 < i \le i_2$ are true for all cohorts, as shown above, and hence are true for the cohorts specified.

It remains to prove the policy for $i < i_1$. Suppose for cohort $i < i_1$ we choose an escapement $y_i < x_i$, and then, the following time period, choose a y_{i+1} optimal for $x_{i+1} = \theta_i y_i$. Our return would be

$$\begin{aligned} &p_i(x_i - y_i) - (c_i/q_i)\ln(x_i/y_i) + \alpha p_{i+1}(\theta_i y_i - y_{i+1}) \\ &\quad - \alpha(c_{i+1}/q_{i+1})\ln(\theta_i y_i/y_{i+1}) + \alpha^2 v_{i+2}''^*(\theta_{i+1} y_{i+1}). \end{aligned}$$

If we increase y_i, we increase $x_{i+1} = \theta_i y_i$ and y_{i+1} will remain feasible. The marginal change with respect to y_i, holding y_{i+1} constant, would be

$$\begin{aligned} &-p_i + c_i/(q_i y_i) + \alpha\theta_i p_{i+1} - \alpha c_{i+1}/(q_{i+1} y_i) \\ &\quad = -p_i + \alpha\theta_i p_{i+1} + (1/y_i)[c_i/q_i \\ &\quad\quad - \alpha c_{i+1}/q_{i+1}] \ge 0. \end{aligned}$$

So, we would do better (at least no worse) to set $y_i = x_i$ and leave y_{i+1} unchanged. Hence, any policy with $y_i < x_i$ for $i \le i_1$ is dominated by a policy with $y_i = x_i$, and thus there must exist on optimal policy with $y_i = x_i$.

Harvesting a cohort down to $\bar{x}_i$ can be termed a "myopic" policy, as it would be optimal for that cohort if the future were disregarded. Since increased escapement cannot decrease our future returns, an optimal policy will never choose to harvest beyond the myopic level.

Note that for cohorts one through i_1 the increase in value of an individual in the water is greater than the dissipation rate through time discounting and natural mortality. Thus, we do not harvest these cohorts ($\delta_i''^*(x) = x_i$). For cohorts $i_1 < i \le i_2$, an individual loses value through time discounting and natural mortality, but gains in availability and cost of capture, and the optimal policy will depend upon the interplay of these influences. We know, however, that we will never harvest beyond the myopic level. For cohorts $i > i_2$, a fish left in the water loses value faster than it gains in cost of capture and a myopic harvesting rule is optimal. Specifically, for cohort n, there is no future and a myopic rule will always be optimal.

For some fisheries the assumption that $c_i/q_i \ge \alpha c_{i+1}/q_{i+1}$ may be restrictive. For example, migrating shrimp may exhibit dramatic increases in c/q as they leave nearshore waters. This assumption can be relaxed somewhat. Note that for cohorts $i > i_2$ we will harvest myopically in spite of decreasing costs of capture. Thus, we will certainly harvest myopically in these cohorts if c/q were increasing. This is stated formally in the following corollary.

Corollary 2.1: The policy results of Proposition 2 remain unchanged if for one or more cohorts $i > i_2$:

$$c_i/q_i < \alpha c_{i+1}/q_{i+1} \text{ and } p_i \ge \alpha\theta_i p_{i+1}.$$

Proof: In the proof of Proposition 2, the result for cohorts $i > i_2$ depends upon showing that

$$\partial J_i/\partial y_i = -p_i + \alpha\theta_i p_{i+1} + (1/y_i)(c_i/q_i - \alpha c_{i+1}/q_{i+1}) \le 0.$$

This result follows immediately under the revised assumptions.

Proposition 2 and Corollary 2.1 completely characterize the optimal escapement policy for cohorts $i \le i_1$ and $i > i_2$. For cohorts $i_1 < i \le i_2$ the results are less exact, due to the competing influences of value and cost of capture. It is possible, however, to completely characterize the optimal policy when this transition phase lasts one time period or less, i.e. if $i_2 - i_1 \le 1$.

Proposition 3: If the hypotheses of Proposition 2 and/or Corollary 2.1 hold, and $i_2 - i_1 \le 1$, then

(1) The optimal policy is as stated in Proposition 2 for $i \le i_1$ and $i > i_2$. If $i_2 = i_1$ this completely characterizes the optimal policy. If $i_2 - i_1 = 1$, then the optimal policy for cohort i_2 is

$$\delta_i''^*(x) = \left(x_i \wedge \frac{c_i/q_i - \alpha c_{i+1}/q_{i+1}}{p_i - \alpha\theta_i p_{i+1}} \right).$$

(2) For all $\delta''^*(x)$, there exists a $\delta'^*(x) \ge \delta''^*(x)$, and for all $\delta'^*(x)$, there exists a $\delta''^*(x) \le \delta'^*(x)$, all x in S.

Proof:

(1) If $i_2 - i_1 = 1$, the proof for $i > i_2$ and $i \le i_1$ remains unchanged from Proposition 2. For $i = i_2$ we have

$$J_i(x_i,y_i) = p_i(x_i - y_i) - (c_i/q_i)\ln(x_i/y_i) + \begin{cases} 0 & \text{if } \theta_i y_i \le \bar{x}_{i+1} \\ \alpha(p_{i+1}(\theta_i y_i - \bar{x}_{i+1}) - (c_{i+1}/q_{i+1})\ln(\theta_i y_i/\bar{x}_{i+1}) \end{cases}$$

otherwise.
Solving for a maximizing y_i over the constraint set $[m_i, x_i]$ yields the result.

TABLE 1. Surf clam model parameter values.

Cohort age (yr)	1	2	3	4	5	6	7	8	9	10
Shell length (cm)[a]	3.8	7.4	9.9	11.7	13.2	14.2	14.7	15.2	15.7	16.0
Weight (g)[a]	3.6	20.4	44.9	70.7	93.9	113.8	129.7	141.9	151.0	158.3
p_i ($U.S.)[b]	0.004	0.022	0.049	0.078	0.103	0.125	0.143	0.156	0.166	0.174
p_i ($U.S.)[c]	0.004	0.022	0.049	0.078	0.110	0.138	0.157	0.172	0.183	0.192
Catchability $q_i = 0.00944$, $i = 1{,}10$										
Marginal cost of effort $c_i = \$165\,358$, $i = 1{,}10$										
Discount rate $\alpha = 0.9$										
Expected survival rate $\theta_i = 0.7945$, $i = 1{,}10$										

[a] Source: Murawski and Serchuk (1979, table 5).

[b] Using $0.0011/g for all cohorts.

[c] Using $0.0011/g for cohorts 1−4, $0.00117/g for cohort 5, and $0.00121/g for cohorts 6−10.

(2) Since problem P'' is separable, and g' is separable, we have

$$V''^{*}\circ g'(y,d) = v_i''^{*}(R) + \sum_{i=2}^{n} v_i''^{*}(d_{i-1}y_{i+1}).$$

Tedious but straightforward calculation, using the policy results from above, show that for $i = 2$ to n, $v_i''^{*}(d_{i-1}y_{i-1})$ is continuously differentiable with respect to y_{i-1} on (m_i, M_i) and that the partial derivative $\partial v_i''^{*}/\partial y_{i-1}$ is a convex function of d_{i-1}. The result follows from Lovejoy (1983, Proposition 4.6).

The first part of Proposition 3 completes the characterization of an optimal policy for problem P'' in the case where $i_2 - i_1 \leq 1$. The second part of the proposition states that in this case an optimal policy for problem P'' provides a rigorous lower bound for an optimal policy for problem P'. As the proof reveals, this result derives primarily from the fact that under the conditions of Proposition 3, $\nabla_y V''^{*}\circ g'(y,d)$ will be convex in d, and hence, $\nabla_y V''^{*}\circ g'(y,\theta) \leq E\nabla_y V''^{*}\circ g'(y,d)$ by Jensen's inequality. That is, the marginal value of fish left to escape is lower in the deterministic model than if g depends upon a random vector d. Under these circumstances, stochasticity makes us more conservative.

The power of Proposition 3 lies in this policy bounding result. Suppose the conditions of Proposition 3 are met, then for any cohort $i \leq i_1$ we have for any state x:

$$x_i = \delta_i''^{*}(x) \leq \delta_i'^{*}(x) \leq \delta^{*}{}_i(x) \leq x_i.$$

Again, equality prevails throughout and $\delta_i^{*}(x) = x_i$. That is, an optimal policy for the full, nonseparable, stochastic problem P will call for the complete abstention from harvesting cohorts 1 through i_1, and this will be true for arbitrary stock−recruitment functions $f(y,d)$ nondecreasing in y, and arbitrary probability distributions for d consistent with the expected value θ.

While model P generalizes those of Clark et al. (1973) and Mendelssohn (1978), the qualitative results are similar. Under reasonable conditions we should forego harvesting as long as the value of a fish in the water is increasing faster than the dissipative effects of time discounting and expected natural mortality. Thus, an age-at-first-capture policy regime extends to this more complex model.

An age-at-first-capture is easily implemented in many fishery systems by regulating mesh size. Thus, we are fortunate in that the mathematically appropriate policy comes in an implementable format. Also, by not requiring detailed knowledge of the stock−recruitment relationship or relevant probability distributions, the bounding procedure is well-suited to the data-sparse environment of fisheries management, where the function f or the distribution of d are often unknown. An example is presented in the next section.

Numerical Example: The Atlantic Surf Clam Fishery

The Atlantic surf clam (*Spisula solidissima*) occupies the benthos throughout the Atlantic shelf region. From Cape Hatteras to Sandy Hook the densities are high enough to support a commerical fishery. Leaving home berths in port towns such as Cape May and Ocean City, surf clam vessels equipped with powerful hydraulic dredges make day trips to hunt the resource. Processors buy the raw input at dockside, and produce chowder, strips, and other clam products. While essentially clams of all sizes can be used for chowders and juices, clams of about 14 cm shell size or larger are necessary for the lucrative breaded strip market. Large clams are therefore more desirable and are actively sought by processors.

The history of the surf clam fishery indicates highly stochastic dynamics, but the relevant distributions are unknown. Also, no empirically justifiable stock−recruitment relationship exists, stochastic or otherwise. Fortunately, this information is not necessary to calculate rigorous policy bounds.

A 10 cohort surf clam model (P) can be constructed using data from the Mid-Atlantic Fisheries Management Council (1981, 1982) and the results of a Sea Grant/University of Delaware surf clam simulation project (Anderson 1982). The relevant parameters are displayed in Table 1. For lack of cohort-specific data, price per gram, expected survival rates, and c/q are assumed constant over all cohorts. Thus, the full generality of Proposition 3 is not invoked, but the policy bounds are no less informative.

Model P would be numerically intractable even if we knew the nature of f and the distribution of d. Suppose, however, we approximate P by assuming constant recruitment and survival rates constant at their expected values. Using this deterministic approximation (P''), it can readily be verified from Table 1 that the conditions of Proposition 3 are met with $i_1 = 3$ and $i_2 = 4$. Thus, we have an age-at-first-capture of 4 yr, or a minimum shell size of 11.7 cm. Furthermore, we have from Propositions 1 and 3 that the effect of adding stochasticity and a stock−recruitment relationship to the model will be to increase this minimum level. Thus, an 11.7-cm minimum shell length is a rigorous lower bound for the regulation appropriate in the actual fishery (as reflected in problem P).

Present regulations in the surf clam fishery call for a minimum shell length of 14 cm, largely as a result of the desires of the processing industry. This limit is not necessarily excessive. Recall that only large clams can be used for the strip market. Let us assume that processors are willing to pay $0.0011/g for cohorts 1−4, $0.00117/g for cohort 5, and

\$0.00121/g for cohorts 6−10. These numbers are hypothetical, as cohort-specific price data are not available. However, the price increase seems modest enough, as the strip market is the most lucrative. The resulting p_i are shown in Table 1, and it can be verified that the conditions of Proposition 3 are satisfied with $i_1 = i_2 = 4$. This implies an age-at-first-capture of at least 5 yr with a minimum shell size of at least 13.2 cm. Thus, the present 14-cm size limit may be justified from a social perspective when economic realities are considered.

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Identifying the Stock–Recruitment Relationship for Age-Structured Populations Using Time-Invariant Matched Linear Filters[1]

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Welch, D. W. 1986. Identifying the stock–recruitment relationship for age-structured populations using time-invariant matched linear filters. Can. J. Fish. Aquat. Sci. 43: 108–123.

Theory is introduced which permits the identification and removal of part of the environmental (density-independent) noise influencing the recruitment to age-structured populations. The biological assumptions under which this noise may be safely removed from the recruitment data without distorting the analysis of the density-dependent dynamics are outlined, and the permissible level of filtering is shown to depend on the age structure of the population in question. As examples of the method, filters were designed and applied to stock–recruitment data available for 16 commercially exploited marine fish populations. A substantial improvement is demonstrated in the statistical precision with which the stock–recruitment relationship can be defined, with standard errors on parameter estimates frequently decreasing by a factor of 2 or 3 after filtering. In general, use of filtering theory should allow a more precise definition of the nature of the stock–recruitment relationship in essentially all age-structured populations.

L'auteur présente une théorie qui permet de déterminer et d'éliminer une partie du « bruit » ambiant (indépendant de la densité) influant sur le recrutement des populations structurées par âges. Les hypothèses biologiques permettant d'éliminer de façon sûre le bruit des données de recrutement, sans distorsion de l'analyse de la dynamique en fonction de la densité, sont brièvement décrites et l'auteur montre que le niveau de filtrage permis dépend de la structure des âges de la population. Comme exemple de la méthode, des filtres ont été conçus et appliqués aux données disponibles sur le recrutement des stocks de 16 populations de poissons marins faisant l'objet d'une pêche commerciale. L'auteur démontre une amélioration appréciable de l'exactitude statistique de la détermination de la relation stock–recrutement, le filtrage permettant fréquemment de réduire par un facteur de 2 ou 3 les écarts types des estimations de paramètres. De façon générale, le filtrage devrait permettre de définir avec plus d'exactitude la nature de la relation stock–recrutement chez pratiquement toutes les populations structurées par âges.

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The inability to define the relationship between stock and recruitment is a serious problem in most fisheries. Predictions of how recruitment will vary as stock size is changed by fishing are often required, as are estimates of the maximum mortality rate that a population can support without collapsing past some arbitrary minimal size. Answers to these types of questions depend on the detection and quantification of the internal density-dependent processes regulating populations.

In most fish populations it appears from circumstantial evidence that density-dependent mortality experienced during the prerecruit stage must form the basis for this regulation (e.g. Shepherd and Cushing 1981). On the other hand, even the question of whether significant density-dependent mortality really occurs in the prerecruit stage is still in some doubt, given the large fluctuations in year-class strength that obscure the shape of the stock–recruitment relationship.

If the influence of stochastic noise on recruitment is large, there is a systematic tendency to overestimate the degree of density dependence in populations whose stock–recruitment relationship is only weakly density dependent (Goodyear and Christensen 1984). There is therefore a real possibility that many fish populations may have collapsed because the strength of the density-dependent mechanisms regulating the population had been overestimated.

Garrod (1973) has in fact suggested that historic levels of exploitation may have exceeded the compensatory ability of many fish populations, so that over the long-term these populations simply fail to perpetuate themselves. And, Parrish and MacCall (1978) and MacCall (1979) have concluded that the estimated stock–recruitment relationships for the Pacific mackerel (*Scomber japonicus*) and California sardine (*Sardinops caerulea*) populations did not confer sufficient stability for the proportionately greater recruitment encountered at low population levels to compensate for the rates of exploitation historically experienced by these stocks.

Unfortunately, the limited precision with which these (and other) stock–recruitment relationships can be defined means that the accuracy of such conclusions is uncertain. In addition, these results were based on the analysis of unusually long time series of data, where the collapse of the fishery was already complete. In such cases a relatively broad range of stock sizes are available for analysis. In practice, it is especially important to identify the stock−recruitment relationship from shorter time series, and before the economic collapse of a fishery is complete.

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This paper introduces theory which improves the identification of the stock−recruitment relationship for many populations. When prerecruit survival is related to the abundance of two or more age-classes, a difference occurs in the relative expression of the density-independent and density-dependent factors affecting recruitment. This effect develops because the variability in individual year-class strengths tends to cancel when averaged, so that a function of two or more age-classes shows less temporal variability than the component age-classes.

This observation forms the basis for a splitting of recruitment variability into two parts: one part that *may* include a component related to density-dependent changes in stock size, and a second part that can *only* be ascribed to the recruitment variability unrelated to changes in stock size (e.g. environmental noise or errors in measuring recruitment). By first removing the unrelated variability it is possible to minimize the influence of density-independent factors on the analysis of the stock−recruitment relationship, and therefore to reduce the potential for estimates of the shape of the stock−recruitment relationship to be largely determined by the unrelated variability present in the recruitment data. Clearly, this possibility can be large when environmental or measurement errors predominate in the recruitment record, as is frequently the case with fisheries data.

I show below that the relative expression of the two components of variability varies with frequency, and can be precisely defined by examining the Fourier transform of the age-classes causing the density-dependent mortality. By first excluding the variability *irrelevant* to the problem of studying the stock−recruitment relationship a clearer evaluation of this relationship becomes possible, but without the necessity for positing an arbitrary mathematical form for the stock−recruitment relationship. The results described below indicate that when reasonable age structure exists in the population, and filtering precedes traditional stock−recruitment analysis, standard errors on stock−recruitment parameter estimates can often be reduced to only one-half or one-third of those obtained using the unfiltered data.

Estimation of Stock

Several definitions of adult stock size have been used in stock−recruitment analyses, with most authors using either adult population numbers or adult population biomass. Both suffer from the obvious limitation that they aggregate many density-dependent population processes in a manner preventing direct study of the prerecruit mortality process. Plotting estimates of the annual number of eggs spawned against estimates of the numbers surviving to recruitment avoids this difficulty, and permits comparison of changes in prerecruit survival with the initial density of the 0-group.

Adult stock is defined here as the population fecundity, or the number of eggs annually spawned by the females (Bagenal 1973). Estimates of population fecundity used later in the paper are calculated by multiplying the annual estimates of female numbers-at-age, obtained from published virtual population analyses, by estimates of the fecundity-at-age. The sources for these data sets, and the detailed assumptions used in estimating the population fecundity, are collated in Appendix B of Welch (1984).

Age-specific fecundity, $m(x)$, is defined here as the product of the fraction of a female cohort that is sexually mature at age x, $\Phi(x)$, and the fertility (eggs per mature individual) of the sexually mature females, $f(x)$. This use of the term fertility is nonstandard and is employed to distinguish between the number of eggs produced by sexually mature individuals and the number of eggs produced by the average individual within a population, $m(x) = \Phi(x)f(x)$.

In several cases, owing to lack of data, it has not been possible to correct for density-dependent changes in adult fecundity rates that may have occurred as population size declined under exploitation (cf. Ware 1980). In such populations the density dependence of population fecundity on adult stock size will be included in the estimates of the density dependence of the prerecruit survivorship on population fecundity reported below.

Assumptions

The development of recruitment filters and testing of stock−recruitment hypotheses requires several nontrivial assumptions. The first is that the distribution of environmental noise with frequency does not change with time, so that its spectral shape is constant. This assumption is of minor concern and is unlikely to be violated on the short time scales normally dealt with in fisheries.

Second, it is assumed that population processes are ergodic, so that time averages of the rate processes influencing the reproductive effort (fecundity, mortality) converge to their probabilistic expectation with large time. It is also assumed that female demographic dominance applies, and the discussion in this paper is always couched in terms of the females — female numbers, female eggs, and adult female vital rates.

Third, survival over the prerecruit period is assumed to depend directly on the density of the 0-group, and it is assumed that other density-dependent influences of the adult stock on prerecruit survival (e.g. cannibalism) are of minor importance. The specification of the transfer function used in the following sections for designing the frequency response of the recruitment filters needs to be modified in populations where density-dependent survival is related to other measures of the adult stock. This problem is considered in a later section.

Finally, it is assumed that the average age-specific distribution of reproductive effort is applicable to the entire history of each fishery. This assumption is false for some of the fisheries because of temporal variation in the level of fishing mortality. Time-varying filters are necessary for a rigorous analysis of the stock−recruitment dynamics of such populations. However, this problem can be readily addressed in practice, and the errors arising from this assumption are neglected in the interest of clarifying the basic theory.

Theory. Time-Invariant Adult Vital Rates

Empirical Influence of Age Structure on Population Fecundity

In order to fix notation, and to appreciate the recursive nature of the recruitment process, it is useful to define the relationship between past and present recruitment levels. A glossary of symbols used in the following development is provided in Table 1.

TABLE 1. Glossary of symbols. A dash indicates a nondimensional quantity.

Symbol	Definition	Dimension
b	Age of first sexual maturation	yr
d	Age of sexual senescence	yr
$E(t)$	Population fecundity in year t	Eggs
f	Subscript, denotes filtered data	Eggs
$f(x)$	Fertility at age x	Eggs/mature female
$F[\cdot]$	Fourier transform	
$F^{-1}[\cdot]$	Inverse Fourier transform	
$h(i)$	Time-domain recruitment filter	—
$H(s)$	Frequency-domain recruitment filter	—
i	$(-1)^{1/2}$, or dummy index	
Im( )	Imaginary part of complex argument	
$k(x)$	Reproductive effort at age x	Eggs/fertilized zygote
$k^\circ(x)$	Conditional reproductive effort at age x	Eggs/recruit
$K(s)$	Fourier transform of reproductive effort distribution	
$\ell(x)$	Survival to age x	—
$\ell^\circ(x)$	Conditional survival to age x	—
L	Filter length	yr
$L(s)$	Fourier transform of stable age distribution	—
$m(x)$	Fecundity at age x	Eggs
$n(x,t)$	Number of x-yr-olds at time t	Nos.
N	Length of time series	yr
N^*	Corrected degrees of freedom	
$N(s)$	Fourier transform of recruitment time series	Nos.
$P[\ ]$	Probability	—
R'	Logarithmic stock–recruitment slope, $\dfrac{d\log_e n(t_r,t)}{d\log_e E(t)}$	—
R'_{crit}	Critical stock–recruitment slope	—
Re( )	Real part of complex argument	—
s	Frequency	yr^{-1}
t	Time	yr
t_r	Age at recruitment	yr
x	Age	yr
$Z(x)$	Instantaneous mortality	yr^{-1}
$\theta(s)$	Phase	Radians
$\xi(s)$	Fourier transform of population fecundity	Eggs
$\sigma^2_{R'}$	Variance of regression estimate R'	—
τ_0	Decorrelation time scale	yr
$\Phi(x)$	Maturity-at-age; fraction of a female cohort sexually mature at each age x	—
$*$	Convolution	
$\vert\ \vert$	Amplitude response, or gain	
$\bar{\ }$	Over-bar, time average	
$^\circ$	Superscript, conditional expectation	

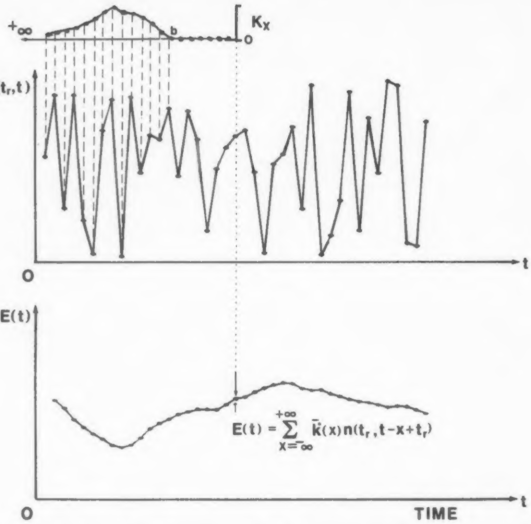

FIG. 1. Graphical representation of the convolution process. The population fecundity is obtained by multiplying the recruitment and reproductive-effort-at-age pairs indicated by broken lines and summing over all products. The population fecundity in year $t + 1$ is obtained by shifting the reproductive effort distribution forward one time step and repeating the process. The recruitment time series illustrated was drawn from a random number generator, and the $k(x)$ values are for the Pacific halibut, Area 3.

Assuming that adult vital rates are time invariant, the probability that a newly recruited t_r-yr-old female survives to some later age x is given by the conditional survivorship function

$$(1)\quad \ell^\circ(x) = \ell(x)/\ell(t_r) = \exp[-(Z(t_r) + Z(t_r + 1) + \ldots + Z(x - 1))]$$

where $Z(x)$ is the instantaneous mortality from age x to $x + 1$, $\ell(x)$ is the survival from spawning to age x, and $\ell^\circ(x)$ is the probability of survival to age x conditional on surviving to recruitment at age t_r.

Given this information on survivorship, it is a simple matter to define the relationship between the population fecundity in a given year and the past recruitment history by reconstructing the age structure of the adult stock from a time series of past recruitments $n(t_r, t)$. The population fecundity $E(t) = n(0, t)$ can then be estimated by multiplying the age-specific fecundity (fertility × maturity) values by the numbers-at-age for females between the ages of sexual maturity (b) and sexual senescence (d):

$$(2a)\quad E(t) = \sum_{x=b}^{d} m(x)n(x, t)$$

or

$$(2b)\quad E(t) = \sum_{x=b}^{d} m(x)\ell^\circ(x)n(t_r, t - x + t_r)$$

where $\ell^\circ(x)n(t_r, t - x + t_r)$ is the estimated number of x-yr-olds alive in year t. For simplicity, it is assumed that sexual maturation occurs at or after recruitment, i.e. $b \geq t_r$.

The product $m(x)\ell^\circ(x) = k^\circ(x)$ is the conditional expectation of reproductive effort at age x, and describes the number of female zygotes that a newly recruited female expects to produce at each future age. For sexually immature or sexually senescent age-classes, reproductive effort is zero, so the summation in (2b) can equally well be taken from $-\infty$ to $+\infty$:

$$(2c)\quad E(t) = \sum_{-\infty}^{+\infty} k^\circ(x)n(t_r, t - x + t_r)$$

or

$$(2d)\quad E(t) = k^\circ(x) * n(t_r)$$

where the asterisk indicates the convolution operator defined by eq. (2c).

Figure 1 sketches this convolution and shows the rela-

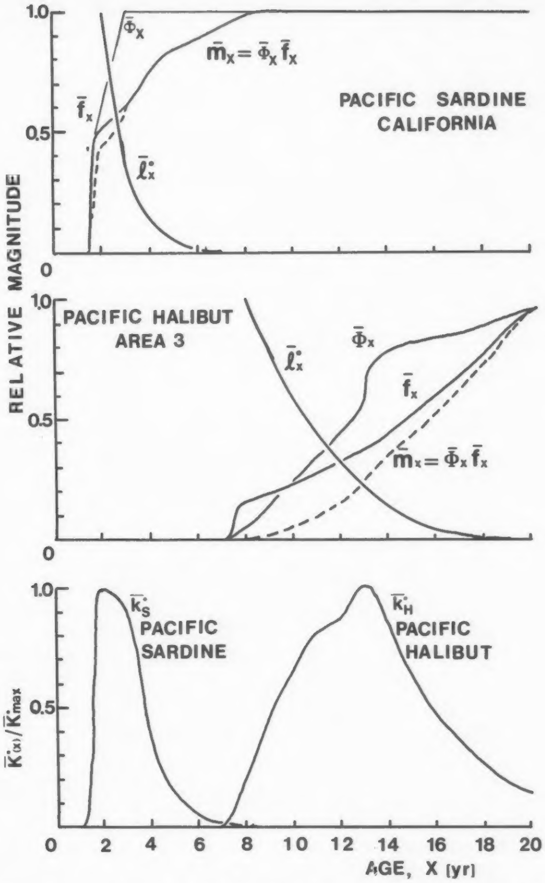

FIG. 2. Comparison of the biological processes determining the female reproductive effort distribution for two different life histories. The upper two panels show the average maturity, $\bar{\Phi}(x)$, average fertility (eggs/mature female), $\bar{f}(x)$, average fecundity (eggs/female), $\bar{m}(x) = \bar{\Phi}(x)\bar{f}(x)$, and average conditional survivorship schedules, $\bar{\ell}^{\circ}(x)$, for Pacific sardine and Pacific halibut.

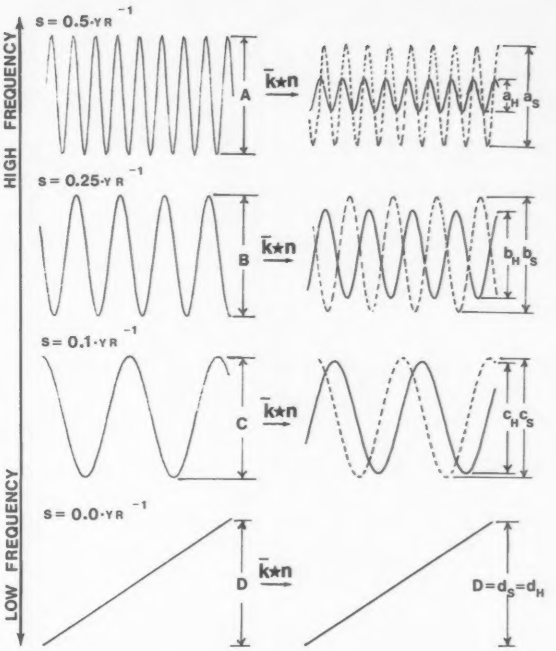

FIG. 3. Influence of two different age structures on attenuating recruitment-induced variability in population fecundity. Four examples are considered, showing the results of convolving the average reproductive effort distributions for the Pacific sardine and Pacific halibut, $\bar{k}^{\circ}_S(x)$ and $\bar{k}^{\circ}_H(x)$, with sinusoids of different frequencies. Attenuation, measured as the ratio of the output to the input sinusoid (e.g. a_H/A in the first example), is a function of both the frequency of the input sinusoid and the form of the reproductive effort distribution.

tionship between the three quantities $E(t)$, $n(t_r)$, and $k^{\circ}(x)$. The convolution operation is simply a moving average over past recruitments, with weights given by the conditional reproductive effort distribution $k^{\circ}(x)$. Depending on the shape of the reproductive effort distribution, a variable degree of smoothing occurs in forming the population fecundity time series.

In Fig. 2 the average $k^{\circ}(x)$ distributions for the Pacific sardine (*Sardinops caerulea*) and Pacific halibut (*Hippoglossus hippoglossus*) are compared to illustrate the importance of the shape of the reproductive effort distribution on smoothing the recruitment. These species represent two extreme life history patterns. Many more age-classes contribute to the halibut's population fecundity than to that of the sardine because the rate of change with age in the halibut's fecundity and survival schedules are approximately equal. Although this is partly due to the lower mortality inflicted on the halibut stock ($\bar{Z} = 0.4 \cdot \text{yr}^{-1}$ vs. $\bar{Z} = 1.1 \cdot \text{yr}^{-1}$ for the sardine), the rates of increase in maturity and fertility with age also play equally important roles in establishing the shape of the reproductive effort distribution, by compensating for the loss in numbers caused by mortality.

The shape of the reproductive effort distribution confers markedly different stability properties on the population fecundity of these two species. To demonstrate this effect, in Fig. 3 the amplitude of several sinusoids is compared before and after convolution with the sardine and halibut reproductive effort distributions. The degree of attenuation in the amplitude of the input sinusoid obviously depends on both the frequency of the input and the type of age structure the input is convolved with. As Fig. 3 indicates, population fecundity is particularly unresponsive to high-frequency variability in recruitment.

The recruitment variability observed in all fish populations is the product of two clearly separable parts. The first is the variation of the population fecundity, which determines the total number of eggs produced each year. The second is the variation is prerecruit survivorship *after* these eggs are spawned. Because population fecundity is an average of past recruitments, it must change relatively slowly, despite occasional sudden changes in recruitment. For this reason, much of the high-frequency variability observed in recruitment time series must be due to either environmental factors affecting prerecruit survival or to error in correctly measuring the true recruitment. On the other hand, population fecundity can vary markedly on long time scales, so observed low-frequency variability in recruitment could result from low-frequency changes in the population fecundity.

The potential for density-dependent changes in prerecruit mortality exists whenever the population fecundity changes. Because population fecundity varies primarily on long time scales, the influence of density-dependent mortality related to changes in stock size must also occur largely on the same time scales. In what follows, this principle is used to develop a method to identify and exclude some of the recruitment variability present in recruitment data sets that is not attributable to density-dependent effects. For convenience, the catch-all term "environment" will be used to denote the variation in recruitment not related to the density-dependent (stock−recruitment) processes of interest. This definition will therefore also encompass errors involved in estimating the annual recruitment.

Calculation of the Transfer Function

Many problems, including the biological convolution described above, yield easily to mathematical analysis using Fourier transform theory (Bracewell 1978). Of particular importance in the present context are (i) the convolution theorem, which states that the convolution of two functions, $n(t)$ and $k(t)$, is equal to the frequency-specific product of their Fourier transforms, $N(s)$ and $K(s)$, and (ii) Fourier's original theorem, which states that any time series can be described as the sum of a series of sinusoids. The discrete Fourier transform and its inverse are defined as

$$(3)\quad \begin{aligned} N(s) &= F[n(t)] = \sum_{t=-\infty}^{\infty} n(t)e^{-i2\pi st} \\ n(t) &= F^{-1}[N(s)] = \sum_{s=-\infty}^{\infty} N(s)e^{+i2\pi st} \end{aligned}$$

where s is frequency, with dimension inverse time, and $i = (-1)^{1/2}$. Defining the Fourier transform of the recruitment and reproductive effort functions as $N(s) = F[n(t)]$ and $K(s) = F[k(t)]$, respectively, the Fourier transform of the population fecundity time series can be written as

$$(4)\quad \xi(s) = F[E(t)] = F[k*n] = K(s)N(s)$$

by virtue of the convolution theorem.

In words, the Fourier transform of the reproductive effort distribution $K(s)$ defines, at a given frequency, the relationship between the variability in the population fecundity and the variability in the past recruitments that form it. This is important information, but to see how it can be used in stock−recruitment analysis it is first necessary to describe some of its properties.

Fourier transforms are described with respect to two frequency-dependent quantities: the amplitude response or gain $|\cdot|$ and the phase $\theta(s)$. For example, the Fourier transform of the average unconditional reproductive effort distribution $\bar{K}(s)$ can be written as

$$(5)\quad \bar{K}(s) = |\bar{K}(s)|\exp[i\bar{\theta}_K(s)].$$

The frequency-dependent nature of the gain and phase in (5) may be obtained by first calculating the complex-valued coefficients of the Fourier transform (using one of the many software packages available, e.g. subroutine FTFREQ of IMSL 1980). Denoting real and imaginary parts of the transform as $\mathrm{Re}(\bar{K}(s))$ and $\mathrm{Im}(\bar{K}(s))$, the gain and phase may be calculated as

$$(6)\quad \begin{aligned} |\bar{K}(s)| &= [\mathrm{Re}(\bar{K}(s))^2 + \mathrm{Im}(\bar{K}(s))^2]^{1/2} \\ \bar{\theta}(s) &= \mathrm{Tan}^{-1}[\mathrm{Im}(\bar{K}(s))/\mathrm{Re}(\bar{K}(s))]. \end{aligned}$$

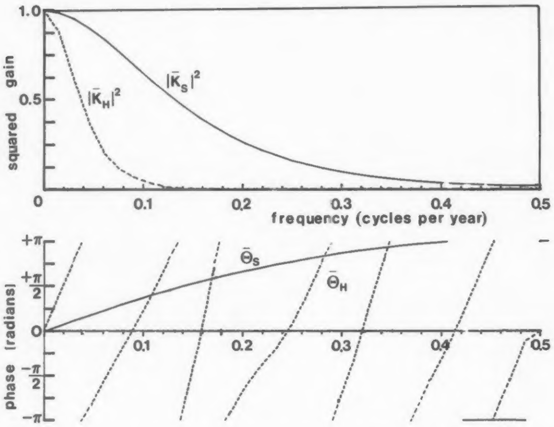

FIG. 4. Comparison of the frequency dependence of the gain and phase of the average transfer functions for the Pacific sardine and Pacific halibut, $\bar{K}_S(s)$ and $\bar{K}_H(s)$.

The Fourier transform of the reproductive effort distribution, $\bar{K}(s)$, is referred to as the frequency response function or transfer function. The square of its gain, $|\bar{K}(s)|^2$, describes the frequency-dependent attenuation in the recruitment variability that occurs in the process of forming the population fecundity. The phase $\bar{\theta}(s)$ describes the time lag before the recruitment variation influences the population fecundity.

The variance in recruitment and egg numbers at a given frequency is given by the square of the corresponding amplitude responses, $|N(s)|^2$ and $|\xi(s)|^2$. These quantities have units $(\text{females})^2$ and $(\text{female eggs})^2$. Without loss of generality, the argument of the Fourier transform may be taken with respect to either the total recruitment or the difference from the mean. In the former case, the frequency-dependent variance will contain a frequency-independent component representing the contribution of the mean to the variance. This component has no influence on the relative gain of the Fourier transform at different frequencies, and therefore has no effect on the design of the ideal filter described below.

Ignoring the phase shift, the relationship between the variance in the time series of recruitment and egg numbers is, by virtue of (4) and (5),

$$(7)\quad |\xi(s)|^2 = |K(s)|^2\,|N(s)|^2.$$

That is, the variance in population fecundity is just a fraction $|K(s)|^2$ of the variance in the recruitment time series. Since the squared gain $|\bar{K}(s)|^2$ can be calculated directly from a knowledge of the distribution of reproductive effort with age, it is possible to use this information to calculate how much of the variance in the recruitment time series is attenuated in the process of forming the population fecundity, as a function of frequency. This information can be used to remove from the recruitment time series a fraction of the total variance that is attributable strictly to environmental influences, and which is unrelated to the density-dependent mechanisms defining the stock−recruitment relationship.

In the sections to follow, it is convenient to normalize the reproductive effort distribution to have an integral value of 1, and to define the transfer function as the Fourier transform of the unconditional reproductive effort distribution

(8) $k(x) = k^{\circ}(x) \Big/ \int_{0}^{\infty} k^{\circ}(x)\, dx.$

This rescaling does not materially effect the results, but does simplify the discussion. Mathematically, normalization ensures that the gain of the ideal filter described below is 1.0 at zero frequency, so that filtering has no effect on any linear trend in the recruitment data.

Calculation of the Attenuation in Recruitment Variance

The squared gain and phase of the transfer functions are compared for the sardine and halibut data in Fig. 4. For both species it is clear that a proportion of the variability present in the recruitment data must be attenuated in the process of forming the population fecundity, although the degree of attenuation differs between species.

The distribution of the total variance in the recruitment and population fecundity time series with frequency, or the power spectrum, is described by the square of the respective amplitude responses, $|N(s)|^2$ and $|\xi(s)|^2$. If the assumption is made that the power spectrum is flat, so that the recruitment variance present per-unit-frequency is equal at all frequencies, then the proportion of the recruitment variance absent from the population fecundity time series is the difference between 1.0 and $|\bar{K}(s)|^2$, integrated over all frequencies. As Fig. 4 indicates, this integral can be a large proportion of the total area.

If all frequencies contained equal variability, the power spectrum would be flat. Experience shows, however, that in all recruitment time series examined much more of the recruitment variability is located at low frequencies. In such cases, estimating the difference in total variability between the recruitment and population fecundity time series as the difference $1.0\text{-}|\bar{K}(s)|^2$ would overestimate the true difference because less of the recruitment variance occurs at higher frequencies, where the age-structure-induced attenuation is greater. To correct for the unequal distribution of recruitment variance with frequency the estimate of the total attenuation in variance must be weighted by the fraction of the recruitment variance present at each frequency.

Figure 5 illustrates the results of this calculation and indicates the proportion of the total recruitment variance which is attributable to environmental influences. The clear area under the lower curve indicates the proportion of the recruitment variance which could possibly be associated with the stock–recruitment mechanisms of interest, and the shaded area indicates the proportion of the variance which is associated purely with environmental factors, and which is *not* related to these mechanisms.

Form of the Ideal Smoothing Filter

Given a recruitment time series with some level of variation $|N(s)|^2$ occurring at a frequency s, the variance in population fecundity is

(9) $|\xi(s)|^2 = |\bar{K}(s)|^2\, |N(s)|^2.$

If $|\bar{K}(s)| = 0$, the form of the reproductive age structure will prevent any variation in recruitment from influencing the population fecundity. And hence, since the egg numbers do not change, all recruitment variation observed at frequency s must be caused by density-independent (environmental) influences on prerecruit survival. Before assessing the form of the density-dependent relationship between stock and recruitment, it is obvious that recruitment variability occurring at such frequencies should be removed.

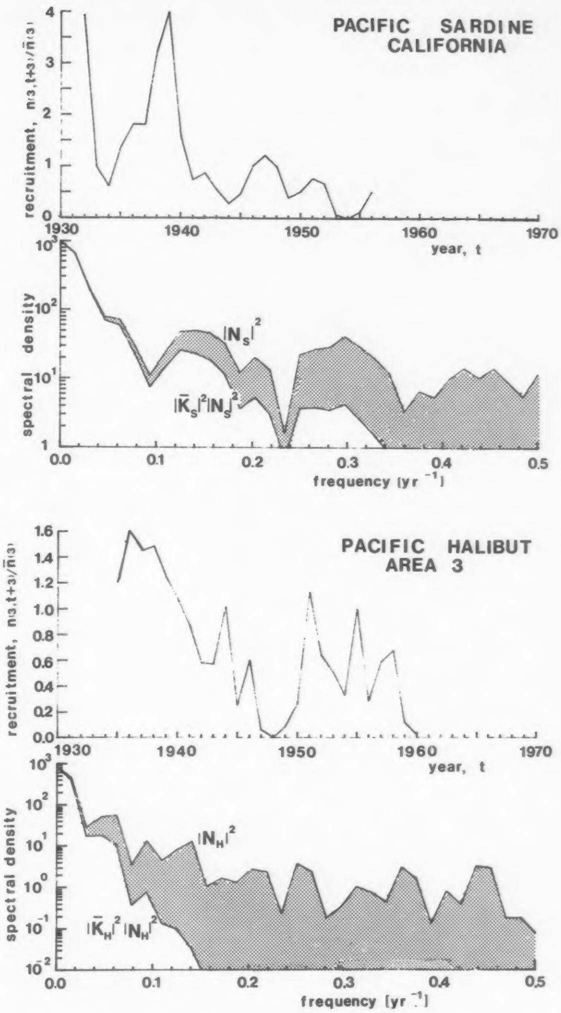

FIG. 5. Recruitment time series for the Pacific sardine and Pacific halibut and their power spectra $|N(s)|^2$. The total variance in the recruitment time series is given by the area under the curve $|N(s)|^2$. The area under the curve $|K(s)|^2|N(s)|^2$ is the recruitment variance remaining in the population fecundity time series. The shaded area represents the proportion of the total recruitment variance strictly attributable to environmental effects, and which should be removed by filtering the data. Note logarithmic scale on ordinate.

In practice, real age structures are unlikely to remove all of the variability in recruitment at any frequency, and some variation in egg numbers will occur. Two distinct situations are possible.

The most likely situation is that $0 < |\bar{K}(s)|^2 < 1.0$, so that some attenuation occurs, and variation in the recruitment is greater than the variation in the population fecundity. In this case it is clear that environmental influences on prerecruit survival must be the cause of the extra variance present in the recruitment time series. The difference $1.0\text{-}|\bar{K}(s)|^2$ represents the proportion of the recruitment variability that must come from environmental factors influencing recruitment after the eggs are spawned, and which needs to be removed. The magnitude of this variance is $(1.0\text{-}|\bar{K}(s)|^2)|N(s)|^2$.

As a second possibility, if $|\bar{K}(s)| = 1.0$, no attenuation occurs and the variation in population fecundity is equal to that in the recruitment time series forming it. In this case it is impossible to identify a fraction of the recruitment variance that is due solely to environmental effects (although, in fact, all of the recruitment variability present might possibly be due to such effects). None of the recruitment variability observed at such frequencies can be discarded prior to stock–recruitment analysis. This will always be so if $s = 0$ because finite age structures cannot attenuate infinitely long wavelengths (cf. Fig. 3).

The problem of studying the relationship between stock and recruitment therefore depends on the design of a mathematical filter which can remove the identifiable environmental noise influencing recruitment without distorting the underlying stock–recruitment dynamics. The preceding paragraphs have shown that a fraction $1.0\text{-}|\bar{K}(s)|^2$ of the recruitment variability present at each frequency should be removed from the time series. This may be achieved by attenuating the variance in the recruitment data to a level

$$(10) \quad |N_f(s)|^2 = |\bar{K}(s)|^2|N(s)|^2$$

of what was originally present at each frequency.

The correctness of the latter statement is ensured by Fourier's theorem, since the variance present at each frequency is completely described by its amplitude and phase. It is therefore possible to accurately filter the recruitment data to remove part of the environmental noise masking the stock–recruitment relationship if a filter can be developed to correctly attenuate the amplitude of the recruitment variation without altering its phase. This result is well known in signal processing theory (Turin 1960, p. 319; Hamming 1962, p. 322), where such filters are often referred to as "matched" filters.

The value $|\bar{K}(s)|^2$ may be thought of as the theoretically "ideal" level at which filtering should stop at each frequency, so that as much of the environmental noise as possible is attenuated without risk of distorting the underlying stock–recruitment signal. If less than the fraction $1.0\text{-}|\bar{K}(s)|^2$ of the recruitment variance is attenuated, some variance unequivocally caused by environmental factors will remain in the recruitment data. On the other hand, if more than the fraction $1.0\text{-}|\bar{K}(s)|^2$ is attenuated, part of the variability in the recruitment data caused by the stock–recruitment mechanisms may be removed. For this reason, attenuating the recruitment variance to the level $|\bar{K}(s)|^2$ of what was originally present at each frequency is the "ideal" level of filtering that should be carried out. More filtering will distort the stock–recruitment signal; less filtering will definitely leave in recruitment variability unrelated to the study of the relationship between stock and recruitment.

It is natural to consider filtering the recruitment data using the transform function $\bar{K}(s)$, since this function has the ideal gain $|\bar{K}(s)|$. However, if this function is used the phase of the filtered recruitment data will be severely distorted because $\bar{\theta}(s)$ is non-zero (cf. Fig. 4, bottom panel). What is required is a filter whose transfer function $H(s)$ is such that the gain approximates the ideal gain as closely as possible, but which has a zero phase shift at all frequencies, i.e.

$$(11a) \quad |H(s)| \geqq |\bar{K}(s)|$$

$$(11b) \quad \theta_H(s) = 0, \qquad 0 \leqq s \leqq 0.5 \cdot \text{yr}^{-1}.$$

Such a filter can be applied to the recruitment data in one of two ways. First, it could be applied in the frequency domain by multiplying the Fourier transform of the filter by the Fourier transform of the recruitment data. Taking the inverse Fourier transform of the frequency-specific products yields the filtered recruitment time series. The filtered recruitment data can then be plotted against the population fecundity to examine the stock–recruitment relationship.

The second approach is to calculate the inverse Fourier transform of the filter's frequency response. This yields the time domain representation of the filter, which is a running mean with a set of weights $h(i)$. Convoluting these weights with the original recruitment time series yields the same filtered time series as the first approach.

By virtue of the convolution theorem, both methods give the same time series, but the second method is computationally simpler and is used here. The major difficulty is to design a filter possessing the desired frequency response (11) while simultaneously satisfying several additional constraints on the form of the filter.

Filter Design

The design of an acceptable recruitment filter requires several facts which are quoted here without proof. The relevant literature is discussed in Hancock (1961), Hamming (1962, 1983), Oppenheim and Schafer (1975), Kaiser and Reed (1977, 1978), and Bracewell (1978).

It is desirable to construct a filter with two basic properties: an odd number of coefficients and even symmetry. (If the midpoint of this filter is at $i = 0$, even symmetry requires that $h(-i) = h(+i)$ for all i.) When these two properties are satisfied the transfer function for the filter $H(s) = F[h(i)]$ is purely real, and the phase shift between the filtered and unfiltered data sets is zero at all frequencies.

If the unfiltered recruitment time series and the filter have lengths N and L, respectively, the length of the filtered recruitment series will be $N - L + 1$ data points long. The reason for this loss of data when smoothing the data is that the filter must fully enter the data series before there is any output. For example, if $L = 3$, the first filtered recruitment point $n_f(t_r, t)$ is calculated as

$$(12) \quad n_f(t_r, t) = \sum_{i=-1}^{+1} h(i)n(t_r, t + i)$$

where the filter is assumed to have its midpoint at $i = 0$. One data point is lost from each end of the time series because the filter averages the recruitment in year t with the recruitment in years $t - 1$ and $t + 1$. In general, a total of $L - 1$ data points are lost when using a filter of length L.

Most stock-recruitment time series are short, and the loss of any data is a serious concern. Recruitment filters need to be designed to minimize this loss of data. Unfortunately, the need for short filters conflicts with the need to remove as much of the environmental noise from the recruitment data as possible prior to stock–recruitment analysis. Increasing the filter length improves the degree to which a filter can be made to approach the theoretically ideal filter, and some compromise between these conflicting requirements must be made.

Few filter design algorithms are sufficiently flexible to meet the requirements of fisheries analysis. Published algorithms (e.g. Kaiser and Reed 1977, 1978; IEEE Press 1979) have been

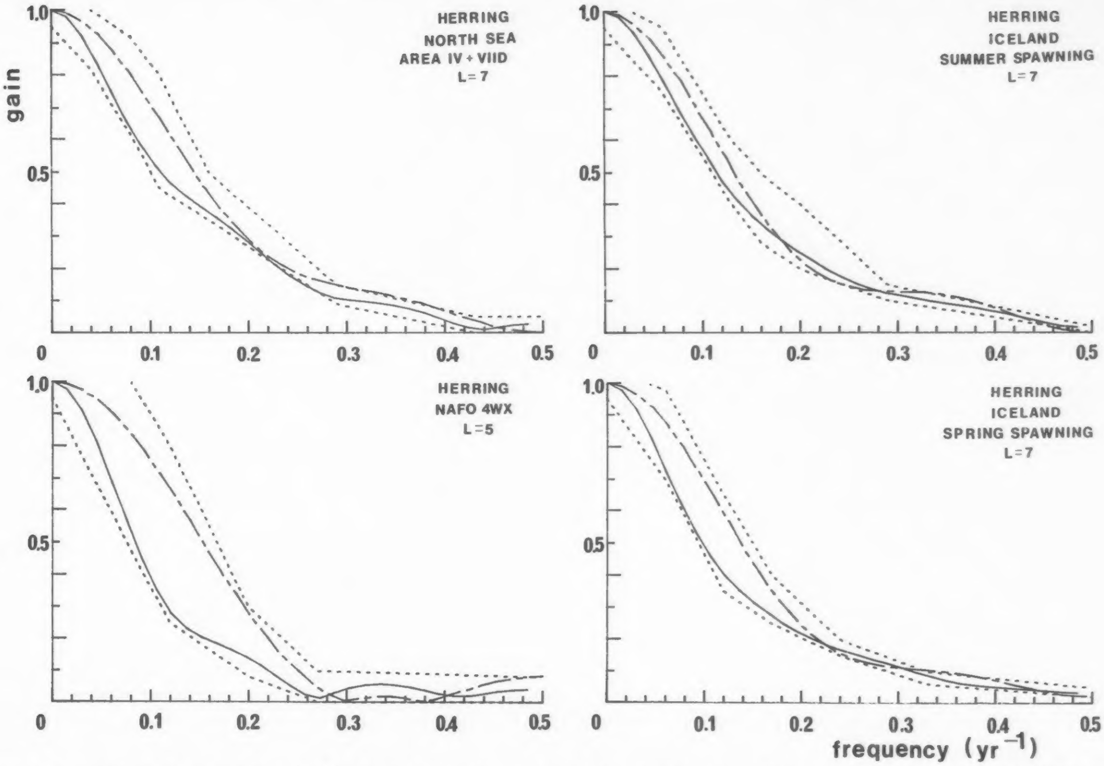

FIG. 6. Comparison of the gain $|H(s)|$ of the filters designed using the simplex algorithm (chain line) and the ideal gain $|\bar{K}(s)|$ (solid line) for herring populations. Broken lines show the final constraints specified on the form of the filter.

developed for use in the physical sciences, where the frequency response of many physical processes is sharply defined. In such situations the objective is to design a filter which passes the input data without modification over some narrow range of frequencies known to contain the signal while completely rejecting the variability occurring at other frequencies.

In a biological context it is usually not possible to establish that all the recruitment variance occurring at certain frequencies is irrelevant to the stock–recruitment problem. However, the theory presented suggests that some filtering is desirable at essentially all frequencies. Normal filter design algorithms do not provide the flexibility necessary for designing acceptable recruitment filters because sufficiently precise control over the frequency-dependent gain of the filter is impossible.

To circumvent the failings of these algorithms a linear programming technique (Rabiner 1972) was used. This algorithm is used as part of an interactive filter design program written to provide the required design flexibility. The program is available from the author.

By means of the simplex (linear programming) algorithm, simultaneous constraints can be specifed on the three important characteristics of the filter: (i) total length L, (ii) evenness (to ensure the phase response is uniformly zero), and (iii) the gain $|H(s)|$. Attributes (i) and (ii) are absolute requirements which the filter must possess. The permissible gain for the filter is specified as a series of upper and lower limits which bracket the theoretically ideal gain $|\bar{K}(s)|$.

A subjective decision as to the maximum allowable filter length is necessary before attempting to design a recruitment filter, which is based on the length of the stock–recruitment time series. The simplex algorithm can then be used to search for a filter which satisfies the constraints (i)–(iii).

If the simplex algorithm fails to find a filter meeting the specified constraints, it can be shown that no filter exists that does so. In such cases it is obvious that either the constraints on the permissible amplitude response $|H(s)|$ must be relaxed or a longer filter specified. Once a filter is found that does satisfy the initial constraints the upper constraint specified on the gain can be reduced in an attempt to improve on the initial solution while maintaining the same filter length. Because of the short filter length necessary, only a few trials are required at this point to minimize the disparity between the gain of the ideal and the designed filters.

In Fig. 6–10 the gains for the recruitment filters designed using this approach are compared with the theoretically ideal gains for 16 major fisheries. The corresponding time-domain filter weights are given in Appendix B of Welch (1984), along with the time-averaged estimates of the reproductive effort characteristics used to calculate the ideal frequency responses. These time averages are based on estimates of the average age-specific fecundity and conditional survivorship schedules for each fishery:

$$\bar{m}(x) = \bar{\Phi}(x)\bar{f}(x)$$

$$\bar{\ell}^{\circ}(x) = \exp[-(\bar{Z}(t_r) + \bar{Z}(t_r + 1) + \ldots + \bar{Z}(x - 1))]$$

with averages calculated over all available data.

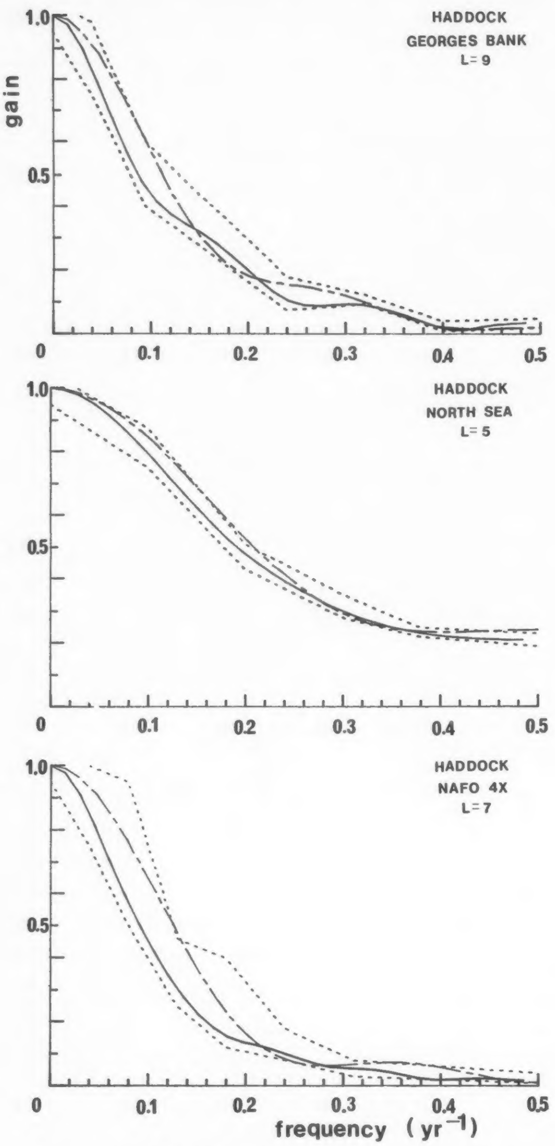

FIG. 7. Gain of the filters designed for haddock populations.

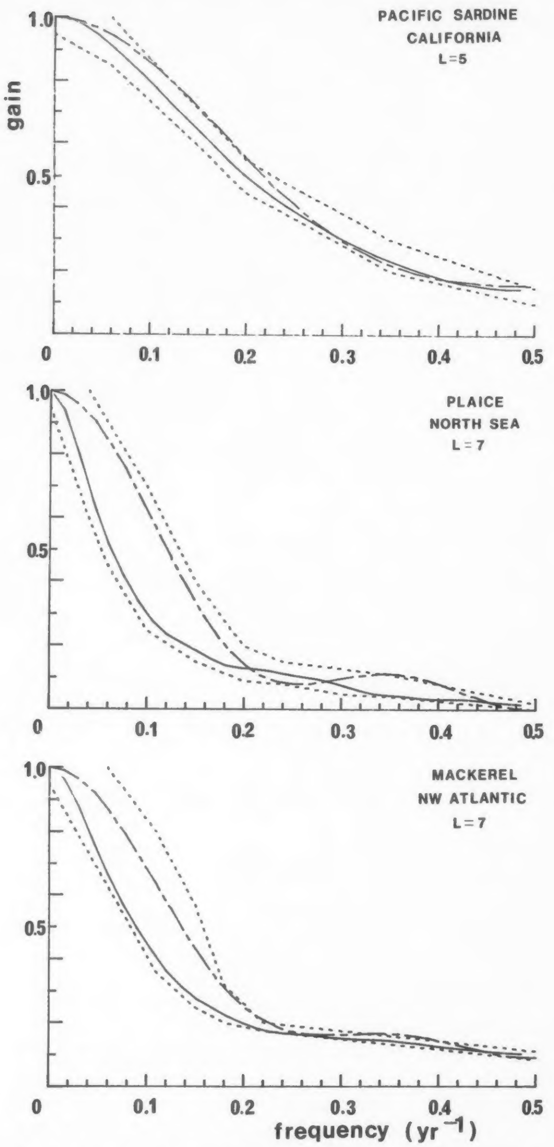

FIG. 8. Gain of the filters designed for Pacific sardine, North Sea plaice, and Northwest Atlantic mackerel populations.

Note that estimates of age-specific fecundity should include estimates of the fertility of sexually mature females, $f(x)$, and estimates of the fraction of an age-class that is sexually mature, $\Phi(x)$. Failure to include information on both the age-specific maturity and fertility schedules can lead to serious underestimation of the level of filtering that is actually possible.

In most cases the major discrepancy between the ideal and achieved gains occurs at mid to low frequencies. This is also where most of the recruitment variance occurs. Efficient removal of this variance is more important than cursory examination of Fig. 6–10 would suggest, partly because the recruitment variance present at low frequencies is often orders of magnitude greater than that at high frequencies (cf. Fig. 5), and partly because the attenuation is equal to the square of the gain. Both factors contribute to inefficient filtering of the environmental variance at low frequency. This means that the filtered recruitment data sets shown later still contain considerably more environmental noise than is theoretically necessary. However, as the results presented below demonstrate, the filters used here still provide a significant improvement in the precision with which a stock–recruitment analysis can be carried out.

Results

An Artificial Example

Monte Carlo experiments were run using model populations

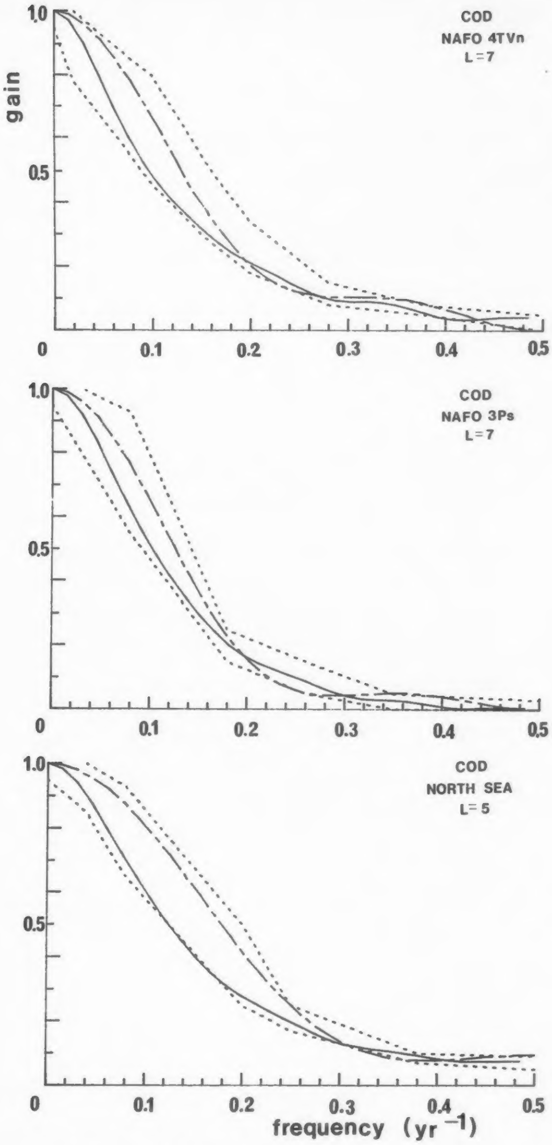

FIG. 9. Gain of the filters designed for cod populations.

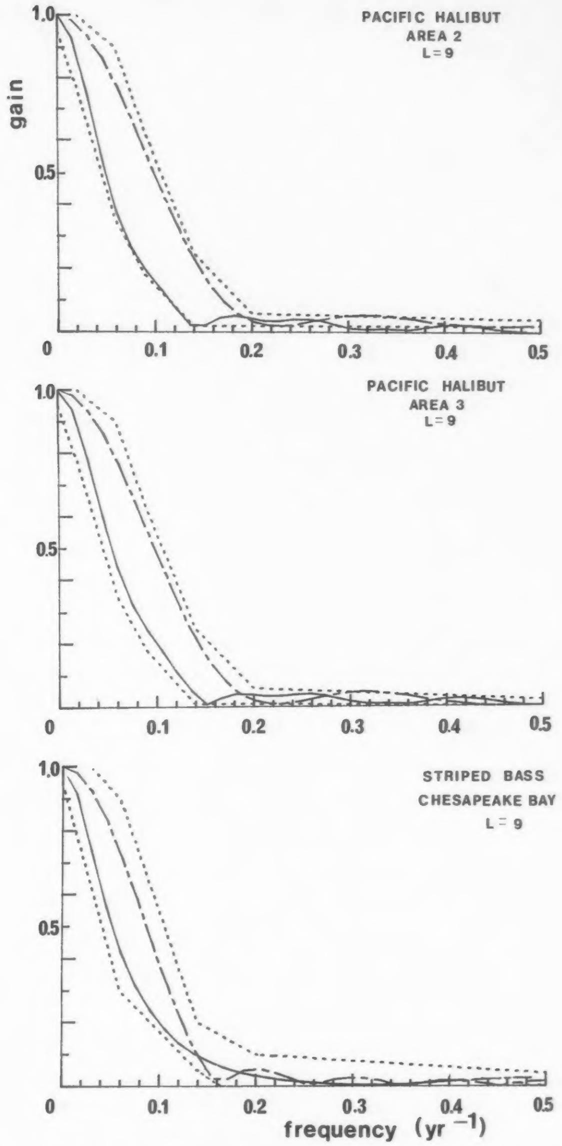

FIG. 10. Gain of the filters designed for Pacific halibut and Chesapeake Bay striped bass populations.

with known stock–recruitment relationships to check the correctness of the foregoing theory. The results from one such experiment are illustrated in Fig. 11. This figure shows the relationship between stock and recruitment from a simulation using the average age-specific vital rates observed for the Pacific halibut in Area 3, but with the instantaneous mortality over the prerecruit period subjected to stochastic perturbations in each model year. The perturbations were specified as normally distributed random variables with mean zero and variance equal to that estimated for the Pacific halibut from the historical record.

Not unexpectedly, the introduction of realistic levels of stochastic noise results in a scatter that makes any specification of the stock–recruitment relationship very uncertain indeed. However, filtering the data with the running-mean filter described in the previous section (cf. Fig. 10) results in a striking improvement in the potential to accurately define the relationship between stock and recruitment, and one that therefore allows much tighter confidence levels to be placed on the parameter values defining this relationship.

The level of improvement observed in this example is extreme, in part because the halibut's age structure permits the design of a filter which removes more of the density-independent noise affecting recruitment than is possible for most populations. In addition, the variance in the random noise terms used here has a relatively flat spectral distribution. In most fish populations, recruitment variance is preferentially

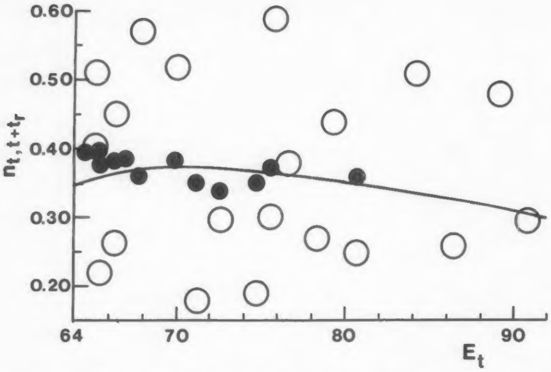

FIG. 11. Filtering results from one Monte Carlo experiment. The solid line shows the true stock−recruitment relationship specified in the simulation model. Open circles represent the recruitment values resulting when the instantaneous 0-group mortality is annually perturbed by a stochastic term with variance equal to that historically observed. Closed circles represent the relationship between stock and recruitment after the recruitment data has been filtered to remove the identifiable environmental noise.

expressed at low frequencies (cf. Fig. 5).

These results demonstrate, however, the substantial improvement possible by filtering the recruitment data prior to analysis. In addition, repeated Monte Carlo experiments support the theory previously outlined, as no evidence of bias was found when the filter's design was based on the correct biological assumptions. Based on 50 Monte Carlo simulations the mean estimate of the density-dependent stock−recruitment parameter differed from the true value specified in the model by only 0.05 standard error. The effect of filtering when the underlying biological assumptions are violated is considered in a later section of this paper

Application of the Filter to Stock−Recruitment Analysis

After an acceptable filter has been designed the recruitment data can be smoothed to remove the identifiable environmental noise and plotted against the population fecundity. Figures 12−16 illustrate the improvement in the stock−recruitment analysis achieved by smoothing the recruitment data with the recruitment filters, and Table 2 summarizes the improvement in the ability to define the relationship between stock and recruitment.

With the exception of the striped bass data set the remaining data sets shown here have been taken from published virtual population or cohort analyses. For the most part these data sources should be reliable, but published stock−recruitment data series can be highly variable. These examples are presented to demonstrate the versatility of the filtering method, and to show the reduction in recruitment variance that can be obtained after filtering. They are not intended as definitive statements about the stock−recruitment dynamics of individual populations until such time as the assumptions used in estimating the population fecundity (Welch 1984) are validated.

It is clear that filtering the recruitment data enhances the ability to identify the stock−recruitment relationship in many fisheries, with a substantial decrease evident in the size of the standard errors on parameter estimates based on the filtered data. The greatest improvement occurs, as expected, in those populations where substantial age structure in the spawning stock is known to exist. In such populations the gain of the ideal filter drops sharply with frequency. As a result, a large fraction of the density-independent recruitment variability may be safely excluded prior to examining the relationship between population fecundity and recruitment. The poorest results are obtained for populations with limited age structure, since the drop in the gain of the ideal filter with frequency is less rapid. In these populations a smaller fraction of the recruitment variability can be attenuated safely prior to examining the relationship between stock and recruitment.

This difference is perhaps most clearly illustrated by comparing the results of the filtering analysis for the North Sea and Georges Bank haddock populations. The decline with frequency in the gain of the ideal filter for the North Sea population is slow compared with the Georges Bank population because a high fishing mortality rate has resulted in a very restricted age structure (Fig. 7). Relative to the Georges bank population, a smaller fraction of the recruitment variability occurring at each frequency can be safely attenuated for this reason, and the relationship between stock and recruitment is defined with poorer precision.

Evidence for Density Dependence in the Stock−Recruitment Relationship

Recruitment will, on average, vary directly with population fecundity if mortality during the prerecruit period is density independent. In this case the expected slope of the stock−recruitment relationship is $R' = +1.0$, when measured using the log-transformed data. Based on the present results several probabilistic statements about the degree of prerecruit density dependence can be made. Assuming that the error about the regression slope R' is normally distributed with variance $\sigma^2_{R'}$ (estimated from the log-transformed and filtered data), then the probability density function for the regression estimate is a *t*-distribution with $N_f^* - 2$ degrees of freedom.

It should be noted that the number of *independent* observations of the stock−recruitment dynamics occurring in the filtered data, N_f^*, is considerably smaller than the number of filtered data points, N_f. The discrepancy between N_f and N_f^* occurs because the density-dependent processes of interest are serially correlated, and, as a result, several years must elapse between independent observations of the stock−recruitment dynamics.

For this reason, assuming that an additional degree of freedom is obtained from each annual observation of the stock−recruitment dynamics will lead to a highly erroneous estimate of the statistical precision of the regression estimates. The details of the calculation of N_f^* are discussed in the Appendix.

When prerecruit mortality is density independent, $R' = +1.0$. If this is true the probability that R' is greater than or equal to 1.0 is 50% because the *t*-distribution is symmetric. However, if prerecruit mortality is density dependent this probability will be lower.

Two other situations of possible interest occur in some of the data sets. The first is the probability that the recruitment slope is negative, $R' < 0$. When this is true the population will undergo low-frequency oscillatory fluctuations in abundance that are driven by the environmental noise. The time scale and number of these oscillations depend strongly on the form of the age structure, and on the sign of the slope of the stock−recruitment curve (Ricker 1954; Allen and Basasibwaki 1974; Botsford and Wickham 1978; Horwood and Shepherd 1981; Welch 1984). The amplitude of these fluctuations can be

TABLE 2. Stock–recruitment parameter estimates and standard errors obtained using the filtered recruitment time series. R' = estimated stock–recruitment slope, R'_f = slope estimated using the filtered recruitment data, N = number of stock–recruitment data pairs available, N_f = number of data pairs remaining after filtering, and N_f^* = estimated degrees of freedom (see Appendix). Probability statements are based on N_f^*-2 df.

	$R' \pm$ SE	$R'_f \pm$ SE	N	N_f	N_f^*	$P[R' < 1]$	$P[R' < 0]$	$P[R' < R'_{crit}]$
Pacific sardine								
California	0.39±0.89	0.33±0.86	25	21	5.8	0.98	0.09	0.00
Striped bass								
Chesapeake Bay	−0.66±2.92	−0.54±2.44	26	18	4.3	0.94	0.77	0.02
Plaice								
North Sea	−0.06±1.63	−1.14±1.21	17	11	4.7	0.98	0.94	0.03
Mackerel								
NW Atlantic	0.48±1.30	−0.06±0.43	12	6	4.9	0.99	0.59	0.00
Pacific halibut								
Area 2	−0.73±0.69	−0.68±0.43	24	16	4.1	0.99	0.96	0.04
Area 3	−1.11±1.28	−0.80±0.70	26	18	5.0	1.00	0.97	0.06
Haddock								
Georges Bank	1.16±4.07	0.47±2.08	42	34	12.1	0.91	0.12	0.00
North Sea	0.05±1.72	0.08±0.89	14	10	6.8	0.99	0.40	0.00
NAFO 4X	−0.24±2.89	−0.39±1.24	13	7	5.1	0.96	0.75	0.02
Cod								
North Sea	−0.24±2.10	0.11±0.86	11	7	5.9	0.97	0.38	0.00
NAFO 3Ps	0.27±1.40	1.45±1.22	15	9	3.7	0.29	0.09	0.04
NAFO 4TVn	0.63±0.61	0.52±0.22	22	16	5.6	0.98	0.01	0.00
Herring								
North Sea	0.20±0.51	0.15±0.14	20	14	3.8	1.00	0.07	0.00
Iceland (spring spawning)	1.20±0.63	0.70±0.89	22	16	3.4	0.76	0.10	0.01
Iceland (summer spawning)	0.93±0.79	0.65±0.38	23	17	5.2	0.92	0.02	0.00
NAFO 4WX	0.70±2.36	0.97±0.20	11	7	4.2	0.53	0.06	0.01

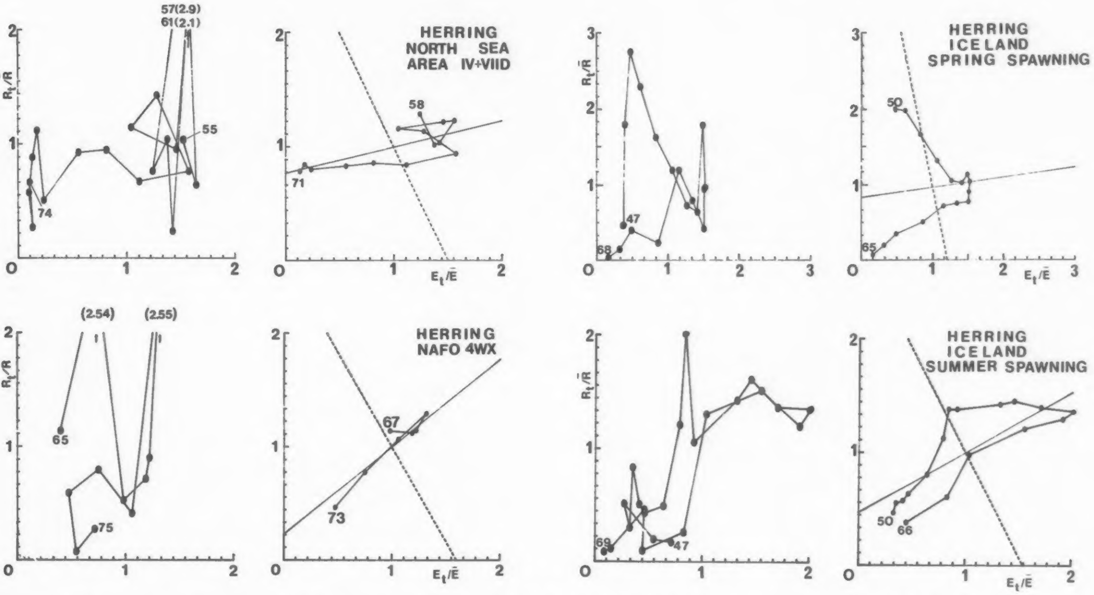

FIG. 12. Stock–recruitment analyses for herring populations. The left- and right-hand panels show, in this and subsequent figures, the relationship between stock and recruitment before (left) and after (right) filtering the recruitment data. Straight lines indicating the proportional recruitment response are indicated by a solid line. A broken line indicates the threshold value for the critical stock–recruitment slope R'_{crit}. Permanent limit cycles in population size will occur for stock–recruitment slopes steeper than R'_{crit}, while at less negative slopes long-wavelength cycles in population size will occur that are driven by the environmental noise.

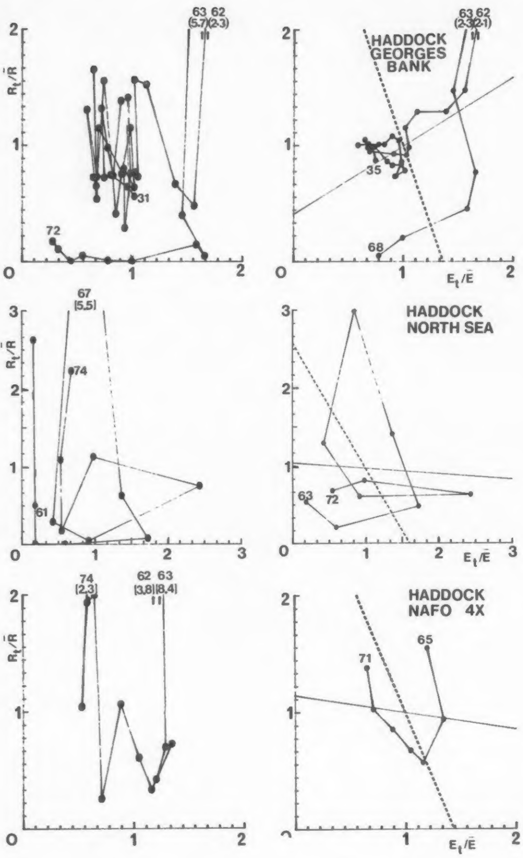

FIG. 13. Stock–recruitment analyses for haddock populations.

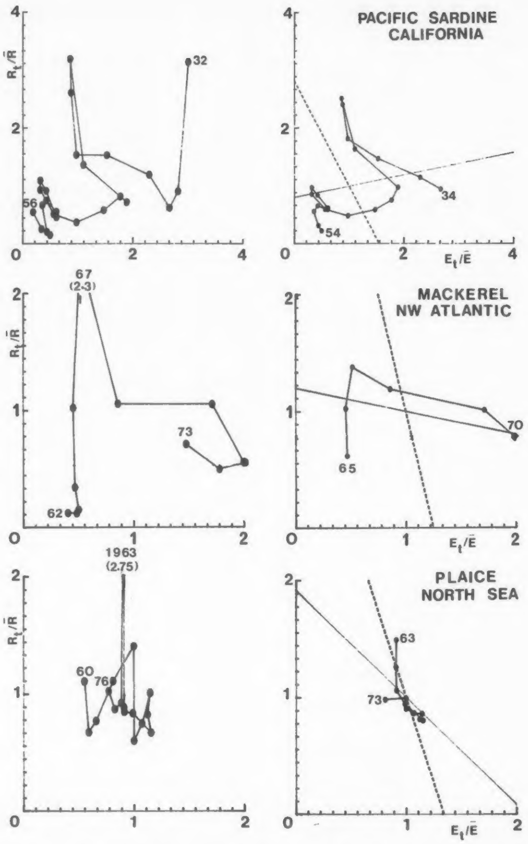

FIG. 14. Stock–recruitment analyses for Pacific sardine, Northwest Atlantic mackerel, and North Sea plaice populations.

damped and the recruitment increased by either increasing or reducing the population fecundity, depending on the sign of the slope of the stock–recruitment curve.

The second situation of interest is the possibility that the recruitment slope exceeds a critical value R'_{crit}. This value may be calculated numerically, using the characteristic equation for age-structured populations (e.g. Botsford and Wickham 1978). When this value is exceeded, permanent oscillations in population size occur.

The results of these calculations are summarized in Table 2, and, strictly as a visual aid, straight lines with slopes equal to the estimated regression slope and R'_{crit} have been drawn through the means of each of Fig. 12–16. Note, however, that the estimates of R' are based on least-squares regression fits to the logarithm of the stock and recruitment data. This transformation is used because it is the proportional change in recruitment which is of interest, and which determines the stability of the population (see Horwood and Shepherd 1981, eq. 5). In addition, taking the logarithm of the data should normalize the errors, since the recruitment variance in fish appears to be log-normally distributed (e.g. Hennemuth et al. 1980; Peterman 1981).

For example, in the first row of Table 2, the probability for the Pacific sardine that survivorship over the prerecruit period was density dependent is calculated to be 98%. Surprisingly, there is about a 1-in-10 chance that stock and recruitment were actually inversely related over the history of the fishery. Given the observed relationship between stock and recruitment, and the documented collapse of the fishery, the latter probability seems quite unlikely. The relatively large probability that an inverse relationship did exist is another example of the rather limited filtering permissible by the theory when the age structure present in the sexually mature sardine stock is severely restricted. The poor statistical precision of the regression estimate that results is a direct consequence of the large variability remaining in the sardine recruitment data after filtering.

In contrast, although the estimated stock–recruitment slope for the Pacific halibut is quite close to the critical value at which permanent limit cycles develop, the probability that the true recruitment response exceeds this value is only about 5%. The higher precision in discriminating between these two similar values is largely attributable to the better filtering of the extraneous variability that theory permits for the highly age-structured halibut population.

Limitations on the Method: Analysis of Semelparous and Stock-Dependent Dynamics

The analysis applied in preceding sections is inappropriate for two types of populations. First, the method will not work

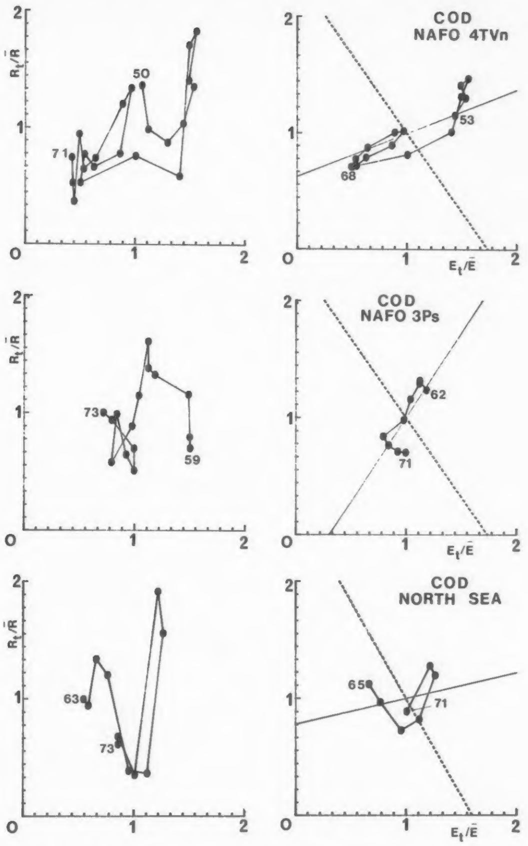

FIG. 15. Stock–recruitment analyses for cod populations.

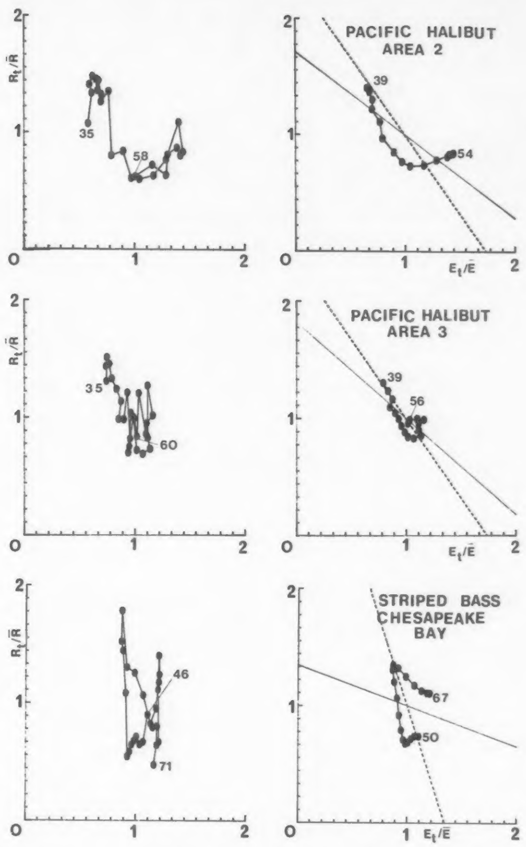

FIG. 16. Stock–recruitment analyses for Pacific halibut and Chesapeake Bay striped bass populations.

for truly semelparous species because there is only one age-class present in the spawning stock. In such cases, no averaging of different year-classes occurs to stabilize the population fecundity, and the Fourier transform of the normalized reproductive effort distribution is uniformly 1.0 at all frequencies.

The pink salmon (*Oncorhynchus gorbuscha*) comes closest to a true semelparous life history strategy among fish because the age of maturation is almost constant, and all individuals die after spawning (Larkin 1977). In all other species of Pacific salmon the age-at-maturity is more variable, and the fecundity of older females is substantially higher (Rounsefell 1957). Thus, although individuals within these populations have a semelparous life history, the breeding structure of the population may exhibit reasonable age structure. It seems likely that the filtering methods used here can be profitably extended to most of the Pacific salmonid species.

The analyses presented here have to be modified if stock-dependent factors such as cannibalism are thought to be of importance in influencing the survival of the prerecruits because the prerecruit mortality is not strictly a function of the 0-group density, as assumed here. Instead, the prerecruit mortality will be a function of some other combination of the age-classes generating the mortality, and the correct argument for the Fourier transform is not the reproductive effort distribution.

To take a concrete example, if cannibalism were thought to have an important influence on the recruitment dynamics it would be necessary to identify the cannibalistic age-groups and the effectiveness of the average individual in these age-groups as a cannibal. In the unlikely event that individuals of all ages were equally efficient, the stock-dependent mortality would be related to the total number of individuals in the cannibalistic age-groups.

The argument of the Fourier transform necessary to establish the form of the ideal filter for studying cannibalistic influences under these assumptions will be $\ell(x)$ (the age-specific survivorship) rather than $k(x) = m(x)\ell(x)$, and the gain of the ideal filter will be $|L(s)|$ rather than $|K(s)|$. Fecundity is an increasing function of age, so the net result is that more age-classes contribute to forming the population fecundity than contribute to forming the cannibalistic population. As a consequence of this simpler age structure, the cannibalistic population will exhibit more variability with time than the population fecundity, and the gain of the ideal filter for studying cannibalism will everywhere be greater than the gain of the ideal filter for studying the 0-group density-dependent processes, $|\mathrm{L}(s)| > |\mathrm{K}(s)|$. Accordingly, a new filter must be designed.

Such a filter can be used to remove the recruitment variability not due to cannibalism, and the filtered recruitment compared with the abundance of the cannibalistic age-groups to establish what relationship, if any, holds between these two variables. If such a filter is not used, and the filter appropriate for studying the density-dependent dynamics is used instead, the empirical relationship between the cannibalistic age-groups and recruitment will be distorted. When this is the case, filtering will improve only the appearance of the analysis while attenuating part of the information present in the data.

In general, the practical difficulty lies in establishing the weighting appropriate to a specific hypothesis, since the basic theory is entirely general.

Discussion

If mortality is density dependent during the prerecruit phase, populations are buffered against external influences and recruitment declines more slowly under fishing pressure than does adult stock size. In such populations a sustainable yield is possible. As the estimates of R' listed in Table 2 show, the strength of this regulation varies both between species and, to a lesser extent, between different populations of the same species.

However, the probability statements summarized in Table 2 demonstrate that in most cases the null hypothesis that prerecruit mortality is density independent ($R' = 1$) can be rejected at the 95% confidence level. That is, prerecruit mortality *does* depend on the density of the 0-group cohort in essentially all populations examined, and a compensatory response to the effects of fishing is therefore to be generally expected in marine fish populations. The degrees of freedom on which the observations on each of these populations are based are very limited, however, and are a matter for deep concern.

Bakun and Parrish (1980) have noted the limited degrees of freedom available in most recruitment records. This problem is further exacerbated in the study of the density-dependent dynamics. Although all data points are included in Fig. 12−16, each plot really contains only a few independent observations on which to base any interpretation of the population dynamics. Effectively, only every N_f^*th data point (Table 2) contributes information on these processes. For this reason, claims of statistical significance for stock−recruitment curves fitted to unfiltered data sets should be viewed with skepticism. Such analyses grossly overestimate the true degrees of freedom available for assessing the reliability of stock−recruitment parameter estimates while retaining much of the recruitment variability unrelated to the stock−recruitment dynamics. This simultaneously overestimates the accuracy of curve fits while reducing the precision of the parameter estimates.

The applications of the filtering theory developed here suggest that a two- to three-fold decrease in the size of standard errors on stock−recruitment parameter estimates is possible when moderate levels of age structure exist in the population. The level of improvement is more modest in populations where an extreme reduction in the age structure has occurred because of fishing, but in most cases is still apparent.

In many of the examples the increase in precision that follows filtering allows reasonable confidence to be placed on estimates of the shape of the stock−recruitment relationship. As the results summarized in Table 2 also demonstrate, such confidence is impossible when using the unfiltered data. In all cases examined confidence limits based on the unfiltered data are far too wide to permit reliable inferences being drawn about the nature of the stock−recruitment relationship.

The weakest aspect of the present methodology involves the practical implementation of the filtering theory. The use of running-mean filters to remove the environmentally induced variability results in the loss of a significant number of data points (typically on the order of 4−8 yr of data), or up to 50% of the time series length in the case of short data records. As a comparison of the gains for the ideal and designed filters shows, these filters also leave substantial variability in the recruitment data which theory suggests should be removed. As confidence limits vary inversely with the square root of sample size, and directly with the residual variance, a more effective method of filtering is clearly desirable. Rough calculations suggest that in some populations, confidence limits could be reduced by a further 50% if a completely effective method of filtering could be implemented.

Summary and Conclusions

By smoothing a recruitment time series it is possible to remove some of the recruitment noise that hinders the identification of the stock−recruitment function. The selection of appropriate filter weights to correctly accomplish this smoothing is based on several biological characteristics of the population and, in particular, on an explicit assumption concerning the nature of the mechanism causing the possible dependence of mortality on population size.

The assumption that mortality experienced during the prerecruit phase is related directly to the 0-group abundance is probably reasonable for many populations. However, as Harris (1975) has shown, an inverse relationship between stock and recruitment cannot be obtained if prerecruit mortality is a direct function of the 0-group density. This raises the interesting possibility that overfiltering has occurred during the analysis of those populations (plaice, Pacific halibut, striped bass) where a negative stock−recruitment slope is indicated, since the basic assumption that prerecruit mortality is density dependent may not be met (see Harris 1975). In each of these populations a probable dependence of growth rate on population density has, however, been documented (Beverton and Holt 1957; Schmitt and Skud 1978; Austin and Hickey 1978), and preliminary considerations suggest that an inverse stock−recruitment relationship may possibly be obtained under this condition (unpublished analysis). These possibilities need further study.

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Appendix: Degrees of Freedom

Averaging adjacent recruitment data points using a set of weights $h(i)$ introduces serial correlation into the structure of the recruitment time series, and results in fewer degrees of freedom than the number of data points would suggest. When confidence limits on the parameters of the stock–recruitment relationship are required, it is necessary to consider the amount of time that must elapse before an independent observation of the stock–recruitment dynamics can be obtained.

A conservative estimate of this time can be obtained from knowledge of the density-dependent dynamics. Following perturbation, recruitment will oscillate with period $2T$ or T yr, where T is the generation length, depending on whether $R' < 0$ or $R' > 0$, respectively (Ricker 1954; Nisbet and Gurney 1982). In this case the decorrelation time scale τ_0 such that the lagged autocorrelation is zero will be, respectively, $\tau_0 = T/2$ and $T/4$ yr.

Density-independent influences on prerecruit survival will usually decorrelate the internal coherence of recruitment time series more rapidly than these estimates suggest. Although this is especially true for the unfiltered time series, it is also true for the filtered data because some environmentally induced variance remains after filtering. In general, these a priori estimates are likely to be of little use except as upper bounds on τ_0, unless low-frequency environmental influences on recruitment are small.

The best strategy is to estimate τ_0 directly from the filtered data. Several suggestions exist in the literature concerning the best way to estimate the corrected degrees of freedom for a data set; Chelton (1983) provides a recent review.

Most methods proved to be numerically unstable when applied to the present data sets, almost certainly because of the short record length available relative to the correlation structure existing within the data. To provide an approximate estimate of the decorrelation time scale, τ_0 was defined as the time to the first zero crossing of the lagged autocorrelation function of the filtered recruitment time series. This is a minimum estimate of the time scale because it does not account for the serial correlation present in the population fecundity time series, or in the cross-correlation structure of the two time series (Bartlett 1946). As a result, the probability estimates listed in Table 2 are overestimates, but the problem is not expected to be severe.

If τ_0 yr must elapse between statistically independent observations of the recruitment dynamics, the number of degrees of freedom on which the parameters describing the density-dependent dynamics are based will be $N_f^* = 1 + (N_f - 1)/\tau_0$, where N_f is the number of stock–recruitment data points available. In general, N_f^* is much smaller than N_f (cf. Table 1). This reflects the fact that if the population fecundity tends to change slowly, next year's population fecundity can be well predicted from this year's population fecundity. Thus, although stock–recruitment data pairs are obtained annually, they "oversample" the density-dependent population dynamics of interest because a few years of new recruitment data add little information on how recruitment changes in response to changes in population fecundity.

Biogeographic Influences on Fish Species Composition of Northern Wisconsin Lakes with Applications for Lake Acidification Studies

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Species–area relations, used to predict the number of fish populations lost in acidified lakes, may overestimate the number of extinctions if regression equations developed from unacidified (high-alkalinity) lakes are used to predict the number of species previously present in acidified (low-alkalinity) lakes. In 100 northern Wisconsin lakes, the species–area regression for alkaline lakes (>10 mg/L as $CaCO_3$) had a higher intercept and greater slope than the regression for low-alkalinity, but unacidified lakes. Thus, low-alkalinity lakes had fewer species than alkaline lakes, and added species at a slower rate as lake size increased. Biogeographic factors (lake size, alkalinity, isolation from other water bodies) strongly influenced fish community composition. Small lake size appeared to exclude species requiring wave-washed, rocky substrates and species preferring cool, well-oxygenated water; such habitat is limited in small lakes. Low alkalinity and associated chemical conditions (e.g. low pH) limited the occurrence of many cyprinids and some percids (genus *Etheostoma*). Lake isolation (no inlet and outlet streams) appeared to have a limited effect on species composition. An exception was the reduced occurrence, in lakes without tributary streams, of species that spawn in flowing water. Fish distributions among Wisconsin lakes provide a test of habitat requirements proposed for other geographic regions.

Les relations espèces – superficie servant à la prévision du nombre de populations de poisson disparues des lacs acidifiés peuvent se traduire par une surestimation du nombre des disparitions si l'on utilise les équations de régression élaborées à partir des lacs non acidifiés (forte alcalinité) pour prévoir le nombre d'espèces antérieurement présentes dans les lacs acidifiés (faible alcalinité). On a noté, pour 100 lacs du nord du Wisconsin, que la droite de régression espèces – superficie des lacs alcalins (>10 mg/L de $CaCO_3$) présentait une coordonnée à l'origine et une pente plus élevées que celle des lacs de faible alcalinité mais non acidifiés. Le nombre d'espèces des lacs de faible alcalinité était donc moins élevé que celui des lacs alcalins et l'augmentation du nombre d'espèces en fonction de l'accroissement de la superficie du lac était aussi plus faible. Les facteurs biogéographiques (taille du lac, alcalinité, isolement des autres plans d'eau) influaient fortement sur la composition de la communauté piscicole. La petite taille des lacs semblait interdire les espèces exigeant des substrats rocheux lavés par les vagues et celles préférant des eaux froides bien oxygénées car de tels habitats sont rares dans les petits lacs. La faible alcalinité et les conditions chimiques qui y sont associées restreignaient la présence de bon nombre de cyprinidés et de certains percidés (*Etheostoma*). L'effet de l'isolement des lacs (absence de tributaire et d'effluent) sur la composition en espèces semblait être limité. Les espèces frayant en eaux courantes étaient cependant moins fréquentes dans les lacs sans tributaire. La répartition des poissons dans les lacs du Wisconsin permet de vérifier les exigences d'habitat proposées pour d'autres régions.

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Relating changes in fish communities to acidification requires a knowledge of community composition prior to acid inputs. For many regions, however, fishery data are sparse or only available for a few lakes or selected species. In the absence of historical data, comparative biogeographic studies can be used to predict fish community characteristics from readily available limnological data (Tonn et al. 1983). For example, species – lake area relations have been used to estimate the number of fish populations that have become extinct in regions receiving acid deposition (Harvey and Lee 1982; Somers and Harvey 1984). The approach has been to develop, by using nonacidified lakes, a regression equation that predicts species richness as a function of lake size. This equation is then used to estimate the number of species that would be expected in lakes prior to acidification. Subtracting the observed from the expected number of species in each lake and summing across all acidified lakes provides an estimate of the number of fish populations lost in the region. A potential problem with this approach is the assumption that species–area relations for the nonacidified lakes (which typically have high alkalinity) and acidified lakes (which presumably had low alkalinity) were similar before acidification. If they were not, and if low-alkalinity lakes always had fewer species than high-alkalinity lakes of similar size, then using the species–area relationship for nonacidified (high-alkalinity) lakes to predict species richness in acidified (low-alkalinity) lakes will result in an overestimate of species losses related to cultural acidification. Using data from 100 Wisconsin lakes and several

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TABLE 1. Lake categories used to examine the influence of morphometric and limnological characteristics on fish community composition in northern Wisconsin lakes. Criteria used to assign lakes to particular categories are described in the text. All values are means (ranges in parentheses) except pH which are medians (ranges in parentheses).

Lake category	*n*	Lake size (ha)	pH	Alkalinity (mg/L as $CaCO_3$)	Number of fish species
I	33	284 (88–1566)	7.1 (6.3–8.6)	28 (15–67)	21 (10–30)
II	17	38 (10–72)	7.3 (6.5–9.2)	52 (15–120)	13 (7–22)
III	11	31 (10–70)	7.2 (6.7–8.1)	24 (12–52)	12 (7–17)
IV	29	22 (5–47)	5.9 (5.1–7.7)	3 (0–9)	7 (4–11)

other lake districts, I examine the conditions under which such overestimates are likely to occur.

Biogeographic analyses have also been used to identify abiotic factors which influence species distributions (Johnson et al. 1977; Tonn and Magnuson 1982; Rahel and Magnuson 1983). In studies of acidified lakes, the goal has been to determine if pH or other abiotic factors are responsible for the absence of particular fish species. In some cases, there has been debate over whether species are missing because of acidification or other habitat limitations (Henderson 1984; Howells 1984). To resolve such conflicts, biogeographic influences on species distributions need to be corroborated by data from a variety of lake districts. Below, I examine the role of lake size, isolation, and alkalinity in structuring fish communities in northern Wisconsin lakes, and relate these findings to biogeographic factors influencing species distributions in other regions.

Methods

Fish species lists, along with morphometric and limnological data (Appendix), were assembled for 100 lakes in north-central Wisconsin.[3] All lakes had summer pH values above 5.0, did not become anoxic in winter, and were not encircled by a bog mat. Recent evidence indicates that these lakes have not been affected by cultural acidification (J. J. Magnuson, University of Wisconsin, Madison, WI, pers. comm.). The lakes had been sampled with at least one type of gear appropriate for small fishes (minnow traps, seines, or 5-mm-mesh fyke nets) and at least one type of gear appropriate for large species (electroshocking, gill nets, trammel nets, or large-mesh fyke nets). Because sampling effort varied among lakes, only presence/absence data were used. Water chemistry measurements were from samples collected just below the surface during summer. Further details on sampling procedures are given by Rahel and Magnuson (1983) and Rahel (1982).

Species–Area Relations

To determine the appropriateness of using the species–area relationship for high-alkalinity lakes to predict species losses in low-alkalinity lakes, I divided the 100 lakes into high- and low-alkalinity groups and compared species–area regressions. A value of 10 mg/L (as $CaCO_3$) was used to separate high- and low-alkalinity lakes because it is near the boundary used to define vulnerability to acidification (Glass 1980; Hendrey et al. 1980). Analysis of covariance was used to determine if the two regression equations had equal slopes and intercepts. The error that might occur if an inappropriate species–area regression was used to predict species losses in acidified lakes was simulated by assuming that all low-alkalinity lakes would become acidified. Various species–area regressions were then used to estimate expected species richness in these lakes. The observed number of species was then subtracted from the predicted number to estimate the accuracy of these regression equations in predicting species richness in low-alkalinity Wisconsin lakes.

Biogeographic Factors and Fish Community Composition

Lake surface area and correlates of productivity (such as alkalinity) have been useful predictors of fish community characteristics in other regions (Ryder et al. 1974; Tonn et al. 1983; Eadie and Keast 1984). To determine their influence on fish communities in northern Wisconsin, the occurrence of each species was examined in bivariate plots of lake area versus alkalinity. To further examine the roles of lake size, alkalinity, and isolation in structuring fish assemblages, I partitioned the 100 lakes into four categories on the basis of morphometric and limnological characteristics (Table 1). Group I consisted of large (≥80 ha), high-alkalinity (>10 mg/L as $CaCO_3$) drainage lakes (i.e., lakes with inlet and outlet streams). These lakes would be the least sensitive to acidification because of their high acid-buffering capacity. They would be expected to have a diverse fish fauna by virtue of their large size, high biological productivity, and connections to other aquatic habitats (Magnuson 1976). Group II consisted of small (<80 ha) drainage lakes having high alkalinity. Lakes in group II differed from those of group I mainly in size and should therefore lack species restricted to large bodies of water. Lakes in group III were similar to those of group II in size and alkalinity but were seepage lakes (i.e. lakes without inlet or outlet streams). These seepage lakes would be expected to lack species that reproduce in streams. Group IV consisted of small, low-alkalinity seepage lakes that were the most vulnerable to acidification and had a depauperate fish community dominated by centrarchids and yellow perch (*Perca flavescens*) (Rahel and Magnuson 1983; Wiener et al. 1984). Ten of the 100 lakes did not fit into any of the four groups and were not used in this analysis. Although

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[3] A complete set of tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

TABLE 2. Use of species−area regressions to predict fish species richness for 33 low-alkalinity ($\leq$10 mg/L as $CaCO_3$) northern Wisconsin lakes. All lakes were from the 100-lake data set discussed in the text.

Regression model	r^2	Number of species−populations for 33 low-alkalinity lakes	Number of excess species−populations predicted for the 33 lakes[b]	Average number of excess species−populations per lake
Regression model based on 67 high-alkalinity lakes[a]				
$Y = 2.67 + 7.15 \log_{10}$ (area)	0.347	414	170	5.2
$Y = 1.76 + 7.20 \log_{10}$ (area) $+ 0.57 \log_{10}$ (alkalinity)	0.348	391	147	4.5
Regression model based on all 100 lakes				
$Y = -1.75 + 8.68 \log_{10}$ (area)	0.496	338	94	2.8
$Y = -2.65 + 7.14 \log_{10}$ (area) $+ 3.39 \log_{10}$ (alkalinity)	0.578	271	27	0.8

[a] Alkalinity >10 mg/L as $CaCO_3$.

[b] Number predicted minus the 244 species−populations present in the 33 lakes.

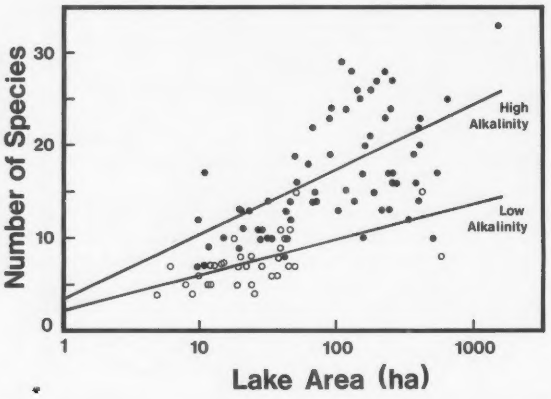

FIG. 1. Relationship between the number of fish species and $\log_{10}$ (surface area) for high-alkalinity (●) and low-alkalinity (○) lakes in northern Wisconsin. The regression equation for the high-alkalinity lakes (>10 mg/L as $CaCO_3$) is $Y = 2.67 + 7.15 \text{ Log}_{10}$ (area) ($n = 67, r^2 = 0.35$) and for the low-alkalinity lakes ($\leq$10 mg/L as $CaCO_3$) is $Y = 2.19 + 3.76 \log_{10}$ (area) ($n = 33$, $r^2 = 0.37$).

it would have been informative to examine fish community composition in other lake types (e.g. small, low-alkalinity drainage lakes), such lake types are uncommon in Wisconsin.

Results and Discussion

Species−Area Relations

Northern Wisconsin lakes with high alkalinity had more fish species than low-alkalinity lakes of similar size (Fig. 1). The slope of the species−area regression was greater for high-alkalinity lakes compared with low-alkalinity lakes ($p = 0.10$, ANCOVA). Although most of the low-alkalinity lakes are also small and lack tributary streams, the relationship between alkalinity and species richness appears to be a general one. Two large, low-alkalinity lakes fall along the same species−area regression line as small, low-alkalinity lakes. Furthermore, when only small seepage lakes were compared, low-alkalinity lakes still had fewer species than high-alkalinity lakes (Wiener et al. 1984).

Given that lakes of different alkalinity have different species−area relationships, it would be inaccurate to use a species−area regression from high-alkalinity lakes to predict species richness in low-alkalinity lakes. For the Wisconsin lakes, the regression for high-alkalinity lakes overestimated species richness by an average of 5.2 species per lake for the 33 low-alkalinity lakes (Table 2). If acidification were to eliminate fish populations in the low-alkalinity Wisconsin lakes, this approach would overestimate by 170 (414 predicted − 244 actual) the number of populations that became extinct. One remedy might be to include an alkalinity term in a multiple regression model. However, this did not greatly improve the model because alkalinity was not strongly related to the number of fish species when only alkaline lakes (>10 mg/L as $CaCO_3$) were used to develop the regression equation (Table 2). An average of 4.5 excess species per lake would still be predicted. A model based on the species−area relationship for all 100 lakes (including high- and low-alkalinity lakes) improved the prediction, and addition of an alkalinity term resulted in the best prediction of species richness (an average of 0.8 excess species per lake predicted for the 33 low-alkalinity lakes). Thus the best model for predicting species richness in low-alkalinity northern Wisconsin lakes incorporated both lake area and alkalinity, and included at least some low-alkalinity lakes. In an acidified region, low-alkalinity lakes having a normal complement of species could be difficult to find. However, historical survey records from even a few low-alkalinity lakes, or species lists from low-alkalinity lakes in nearby regions with similar fish faunas, could be used to develop an appropriate regression model to predict species richness from morphometric and limnological conditions.

Contrary to results for the Wisconsin lakes, alkalinity was not a useful predictor of fish species richness in four other groups of North American lakes (Table 3). Only for the Florida lakes did an alkalinity term measurably improve the amount of variation accounted for by the regression model, and then only by 4%. Somers and Harvey (1984) had used the species−area regression for 34 unacidified lakes near Wawa, Ontario, to predict species losses from 16 lakes acidified by nearby smelting operations. Their model accounted for 33.5% of the variation in species richness among lakes, and inclusion of an alkalinity term did not improve the regression. Furthermore, whereas the partial correlation between the number of species and the logarithm of alkalinity (after removing the effect of lake size) was significant for the 100 Wisconsin lakes ($r = 0.40$, $p < 0.01$), it was not significant for the 34 Wawa lakes ($r = -0.02$, $p = 0.91$).

The lack of a relationship between species richness and alkalinity in lakes from the Experimental Lakes Area (northwestern

TABLE 3. Regression models used to predict fish species richness from lake size

Region, number of lakes (in parentheses), and regression equations used to predict species richness	r^2	Signifi of t alkali coeffi (*p*
Northern Wisconsin (100)		
$Y = -1.75 + 8.68 \log_{10}$ (area)	0.50	—
$Y = -2.65 + 7.14 \log_{10}$ (area) $+ 3.39 \log_{10}$ (alkalinity)	0.58	<0.
Wawa, Ontario (34)		
$Y = -0.70 + 5.80 \log_{10}$ (area)	0.34	—
$Y = -0.49 + 5.79 \log_{10}$ (area) $-0.15 \log_{10}$ (alkalinity)	0.34	0.
Experimental Lakes Area, northwestern Ontario (54)		
$Y = -0.01 + 4.33 \log_{10}$ (area)	0.63	—
$Y = -0.38 + 4.09 \log_{10}$ (area) $+ 1.21 \log_{10}$ (alkalinity)	0.64	0.
Manitoulin Island (44)		
$Y = 1.43 + 5.49 \log_{10}$ (area)	0.64	—
$Y = -13.84 + 5.68 \log_{10}$ (area) $+ 5.60 \log_{10}$ (alkalinity)	0.65	0.
Northern Florida (34)		
$Y = 0.95 + 5.98 \log_{10}$ (area)	0.45	0.
$Y = 2.65 + 4.37 \log_{10}$ (area) $+ 3.03 \log_{10}$ (alkalinity)	0.49	

[a] Partial correlation between species richness and $\log_{10}$ (alkalinity) after remov

ake size and alkalinity.

Significance of the alkalinity coefficient (p)	Partial correlation (r) between species richness and and alkalinity[a]	Alkalinity range (mg/L as $CaCO_3$)	Range of species richness	Predicted species richness for 100-ha lake	Reference
—	0.40	0−120	4−33	15.6	Present study
<0.01					
—	−0.02	0.4−8	3−15	9.9	Sommers and Harvey 1984
0.91					
—	0.19	0.3−11	1−12	8.7	Beamish et al. 1976
0.16					
—	0.16	70−216	2−27	9.6	Harvey and Coombs 1971; Harvey 1978
0.31					
0.12	0.28	0−131	4−28	12.9	Keller 1984

r removing effects of $\log_{10}$ (lake area).

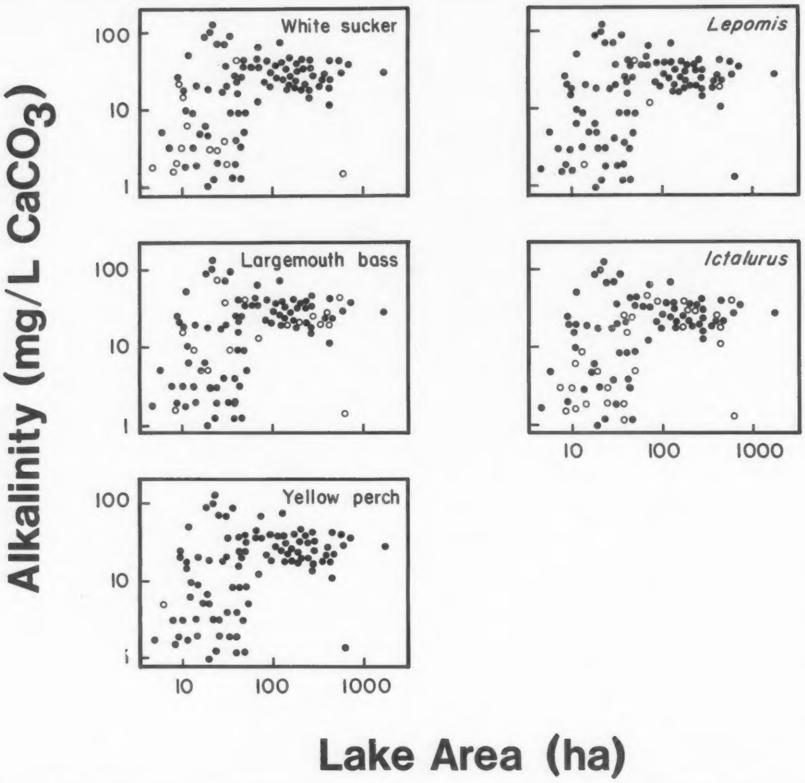

FIG. 2. Fish species common across the entire range of lake area and alkalinity present among 100 northern Wisconsin lakes. Species presence is denoted by (●) and absence by (○).

Ontario) and Manitoulin Island may be a result of the narrow range of alkalinity present in those regions. Only low-alkalinity lakes occur in the Experimental Lakes Area and only high-alkalinity lakes occur on Manitoulin Island (Table 3). A high correlation between species richness and lake alkalinity would only be expected when a relatively wide range of alkalinity is present. For example, the partial correlation coefficient between alkalinity and species richness (after the effect of lake area was removed) was high when all 100 Wisconsin lakes were considered ($r = 0.40$, $p < 0.01$), but was low when the 67 high-alkalinity lakes ($r = 0.02$, $p = 0.85$) or the 33 low-alkalinity lakes ($r = 0.13$, $p = 0.48$) were considered separately. This may also explain the low correlation between species richness and alkalinity for the Florida lakes. Although the range in alkalinity was great (0−131 mg/L as $CaCO_3$, Table 3), 31 of the 34 lakes had an alkalinities below 10 mg/L. If additional alkaline lakes were examined, the relationship between species richness and alkalinity might be strengthened.

Relationships between diversity and measures of lake productivity have been noted in some lake districts. In a study of 14 lakes in central New York, Browne (1981) reported a significant correlation ($r = 0.68$, $p < 0.05$) between the number of fish species and three limnological characteristics related to lake productivity: average Secchi disk reading and chlorophyll *a* concentration in summer and average total phosphorus concentration in winter. However, there was no indication of how community composition changed along this gradient. In Lake Memphremagog, Quebec−Vermont, diversity of the littoral fish community was positively correlated with a nutrient−production gradient (Gascon and Leggett 1977; Nakashima et al. 1977). The abundance of individual species was principally governed by the abundance of preferred food. Few species were absent from the lower end of the productivity gradient, although many were rare. This may reflect the continual dispersal of individuals from productive to unproductive areas, as was hypothesized for young eastern silvery minnows (*Hybognathus regius*) (Gascon and Leggett 1977). Thus, many species may persist in unproductive environments because of continual immigration from more productive areas.

The degree to which alkalinity and other measures of lake productivity are related to species richness in other regions needs to be examined further. However, the existence of such a relationship in some regions (e.g. northern Wisconsin and central New York) indicates that some measure of productivity should be considered when regression models, developed for one group of lakes, are used to predict species richness in lakes with different morphometric and limnological characteristics.

Biogeographic Factors and Fish Community Composition

White suckers (*Catostomus commersoni*), largemouth bass (*Micropterus salmoides*), sunfish (*Lepomis* spp.), bullheads (*Ictalurus* spp.), and yellow perch were common across the entire range of lake size and alkalinity (Fig. 2) and were the major species present in small, low-alkalinity seepage lakes in northern Wisconsin (group IV, Table 4). Seepage lakes of similar size, but with higher alkalinity (group III), contained

TABLE 4. Comparison of fish species composition among 90 Wisconsin lakes differing in surface area, alkalinity, and isolation. Values are the percent of lakes within a lake category containing a given taxon. All lakes had summer pH's above 5.0 and were not anoxic in winter. See text for scientific names.

	Lake category[a]			
	I (n = 33)	II (n = 17)	III (n = 11)	IV (n = 29)
Taxa common in all lake types (% occurrence)				
Catostomidae				
White sucker	100	94	82	69
Centrarchidae				
Largemouth bass	88	82	82	86
Lepomis spp.	100	100	82	97
Ictaluridae				
Ictalurus spp.	85	82	91	59
Percidae				
Yellow perch	100	100	100	97
Taxa less common in small, low-alkalinity lakes than in other lake types (% occurrence)				
Centrarchidae				
Rock bass	91	65	55	24
Cottidae				
Mottled sculpin	64	29	27	0
Cyprinidae				
Notropis spp.	85	41	55	0
Pimephales spp.	88	35	82	0
Esocidae				
Northern pike	100	88	55	34
Percidae				
Etheostoma spp.	82	53	64	0
Taxa generally less common in small lakes than in larger lakes (% occurrence)				
Catostomidae				
Moxostoma spp.	55	24	0	0
Centrarchidae				
Smallmouth bass	85	18	55	21
Black crappie[b]	85	88	55	38
Cyprinidae				
Golden shiner	82	82	36	34
Esocidae				
Muskellunge	88	35	18	3
Gadidae				
Burbot	67	12	18	0
Percidae				
Logperch	42	6	18	0
Walleye	100	47	64	21
Percopsidae				
Trout-perch	33	0	0	0

[a] I, large, high alkalinity, inlets/outlets present; II, small, high alkalinity, inlets/outlets present; III, small, high alkalinity, inlets/outlets absent; IV, small, low alkalinity, inlets/outlets absent (see text and Table 1 for further description of categories).

[b] *Pomoxis nigromaculatus*.

this core group of species plus mottled sculpin (*Cottus bairdi*) and several species of minnows and darters. These additional species seemed to be restricted to waters that had at least moderate alkalinity and a circumneutral pH (Fig. 3). Based on evidence from laboratory bioassays, species distributions among naturally acidic lakes and species losses from culturally acidified lakes, mottled sculpins, and many minnows and darters appear to be intolerant of low pH. For example, minnows (*Pimephales* spp., *Notropis* spp.) and darters (*Etheostoma* spp.) were absent below pH 6.0 in naturally acidic Wisconsin lakes even when appropriate habitat was present (Rahel and Magnuson 1983). The sensitivity of these species to low

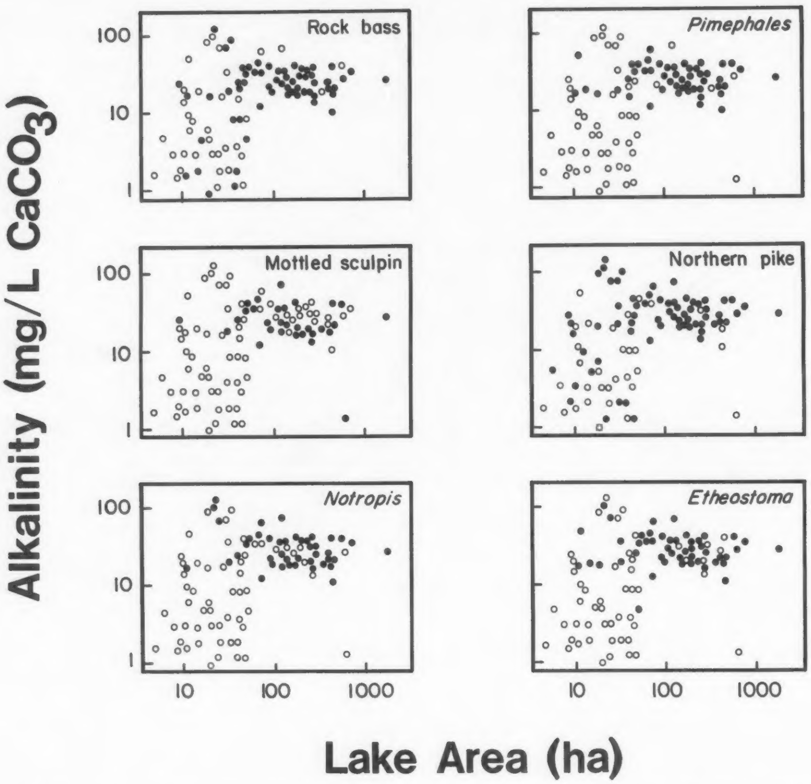

FIG. 3. Fish species less common in small, low-alkalinity northern Wisconsin lakes than in other lake types. Species presence is denoted by (●) and absence by (○).

pH has also been demonstrated in laboratory bioassays (Mount 1973) by field manipulations of pH (Mills 1984) and by distribution studies (Hastings 1979). Because of their intolerance of low pH, these species have probably always been absent from small, low-alkalinity lakes having pH values below 6.0 (Table 1). However, because these species were also absent from small, low-alkalinity seepage lakes with neutral pH, biotic interactions may have also been involved. The paucity of mottled sculpins, cyprinids, and darters in small, oligotrophic lakes has been attributed to both predation and competition from centrarchids and yellow perch (Rubec 1975; Tonn and Magnuson 1982; Rahel 1984).

The low frequency of occurrence of rock bass (*Ambloplites rupestris*) and northern pike (*Esox lucius*) in small, low-alkalinity seepage lakes was not the result of acid sensitivity, since both species are acid tolerant (Harvey 1980). Reasons for the rarity of rock bass are unknown, but northern pike are probably limited by a lack of vegetated littoral areas needed for spawning (Becker 1983). The lack of vegetation represents an indirect effect of low pH and low alkalinity on fish distributions because these water chemistry conditions are associated with low nutrient levels that result in sparse aquatic vegetation.

While minnows, darters, and mottled sculpin were probably absent from low-alkalinity seepage lakes because of both direct and indirect effects of low pH and associated water chemistry conditions, the rarity of other species appears to be related to small lake size. Smallmouth bass (*Micropterus dolomieui*), muskellunge (*Esox masquinongy*), burbot (*Lota lota*), logperch (*Percina caprodes*), walleye (*Stizostedion vitreum vitreum*), and trout-perch (*Percopsis omiscomaycus*) were less common in small lakes than in large lakes (Fig. 4; Table 4). Except for muskellunge, these species require wave-washed, hard-bottomed substrate as habitat or spawning sites (Becker 1983). Such habitat is limited in small lakes, which generally have little wave action. Burbot prefer cool, well-oxygenated water and would not be expected in small lakes that are warm due to polymixis or have cool water only in an anoxic hypolimnion during the summer.

Lake isolation appeared to have little effect on fish community composition. Small, high-alkalinity lakes with inlet and outlet streams (group II, Table 4) had fish assemblages similar to those in small, high-alkalinity lakes lacking such streams (group III). The limited effect of lake isolation may have two causes: some seepage lakes have occasional connections to other water bodies during periods of high water, and fish introductions by man are common in northern Wisconsin lakes (Rahel 1982, 1984). Hence, lack of colonization opportunities may not be as important in limiting species richness in seepage lakes as previously thought. However, species that utilize tributary streams for spawning or as a refuge from predators would still find it difficult to persist in seepage lakes. Redhorses (*Moxostoma* spp.) and golden shiners (*Notemigonus crysoleucas*) may be examples of such species. Redhorses occurred in a few small drainage lakes (group II), but not in small seepage lakes. These fish spawn in stream riffles and thus their absence from seepage lakes was likely related to a lack of

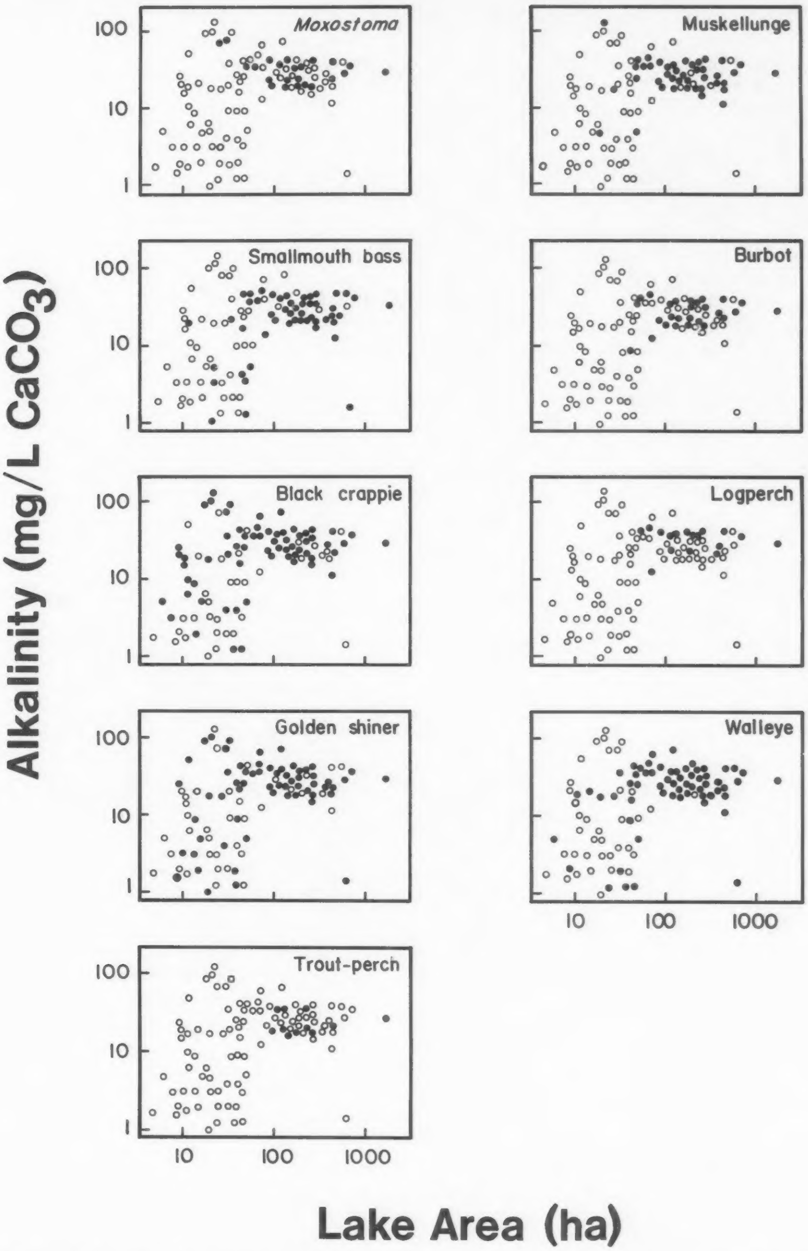

FIG. 4. Fish species less common in small northern Wisconsin lakes than in larger lakes. Species presence is denoted by (●) and absence by (○).

access to appropriate spawning areas. Golden shiners were more common in small drainage lakes than in small seepage lakes and this may reflect the fact that inlet and outlet streams can provide a refuge for species that might otherwise be eliminated from lakes by predators or competitors. Moyle (1973) suggested that some minnow species thought to be competitively inferior persisted in a Minnesota lake because they could maintain a high population in a tributary stream.

Examining species composition in lakes partitioned on the basis of size, alkalinity, and isolation helps to clarify reasons for the absence of many species from small, low-alkalinity seepage lakes in northern Wisconsin. Previous conclusions that certain species were absent because of low pH (Rahel and Magnuson 1983; Wiener et al. 1984) still apply to darters of the genus *Etheostoma* and most cyprinid species. The rarity of other species now appears to also result from small lake size (e.g. muskellunge, burbot, logperch, trout-perch, walleye) or the absence of tributary streams (e.g. redhorses).

Although comparative biogeographic studies can offer insights into environmental factors limiting species distributions, results must be viewed with caution. For example, Henderson (1984) listed the presence of a tributary stream as a habitat requirement for bluegills (*Lepomis macrochirus*) in the La Cloche mountain lakes of Ontario. There is little evidence from autecological studies to support this habitat requirement (Becker 1983), and this species is found in most seepage lakes in northern Wisconsin (Table 4). Similarly, a requirement of calcium concentrations above 4 mg/L for yellow perch in the La Cloche lakes contrasts with the presence of yellow perch in many Wisconsin lakes, including naturally acidic bog lakes, that have calcium concentrations below this level (Rahel 1983; Wiener 1983). These discrepancies may reflect the fact that habitat requirements may change after a lake has been acidified. Calcium is known to counteract the harmful effects of acid exposure in fish (Wood and McDonald 1982), and thus species may require high calcium concentrations to survive in acidified lakes of the La Cloche region. However, it would be misleading to interpret this as a general habitat requirement that limits species distributions in nonacidified lakes. In another example, adults of some species tolerate pH levels that are lethal to larval stages and therefore populations may only persist in acidified lakes if there is access to nonacidified tributary streams for reproduction (Muniz and Leivestad 1980). Thus, the presence of tributary streams may be a habitat requirement for species in acidified lakes, but not in nonacidified lakes where in-lake spawning is possible.

Conclusions about which environmental factors limit species distributions will be strongest when studies involving numerous geographic regions identify similar limiting factors. For example, the restriction of walleyes to larger lakes has been reported by numerous investigators and probably reflects the need for wave-washed, rocky shoal areas for spawning (Johnson et al. 1977; Henderson 1984; present study) Also, the rarity of minnows and darters below pH 6.0 in the La Cloche lakes (Harvey 1980) agrees with similar limitations evident in northern Wisconsin lakes and streams of the New Jersey Pine Barrens (Hastings 1979; Rahel and Magnuson 1983).

Analysis of fish distributions among northern Wisconsin lakes has identified species that are present across a wide range of lake size and alkalinity (white sucker, largemouth bass, sunfish (*Lepomis* spp.), bullheads (*Ictalurus* spp.), and yellow perch). Also evident were species uncommon in small lakes (smallmouth bass, muskellunge, burbot, logperch, walleye, and trout-perch), or lakes with low-alkalinity (minnows, darters, and mottled sculpin), or lakes lacking tributary streams (redhorses). These habitat relations should be useful in predicting the fish community composition expected in other north-temperate lakes, and in determining if particular species are absent from acidified lakes because of low pH or other habitat limitations.

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APPENDIX: Morphometric and limnological data for the 100 study lakes. Further information can be found in Rahel (1982), Tonn and Magnuson (1982), and Wiener et al. (1984).

Lake	County[a]	Area (ha)	Maximum depth (m)	pH	Alkalinity (mg/L as $CaCO_3$)	Tributary stream(s)[b]	Number of fish species
1. Alder	V	110.9	10.1	7.4	33.0	Y	29
2. Alice	L	554.0	9.8	7.2	28.0	Y	17
3. Allequash	V	163.9	10.1	7.8	39.0	Y	20
4. Bear	F	27.5	7.3	8.1	70.0	Y	11
5. Bearskull	I	31.2	8.2	6.5	35.0	Y	10
6. Benedict	V	10.5	5.0	6.1	2.0	N	6
7. Big Fork	O	252.5	6.7	6.9	17.0	Y	24
8. Big Muskellunge	V	373.5	19.8	8.4	21.0	N	19
9. Big Pine	I	255.8	6.7	6.8	15.0	Y	16
10. Big Portage	V	258.2	12.2	7.2	16.0	Y	17
11. Big Saint Germain	V	654.4	12.8	7.2	35.0	Y	25
12. Big Stone	O	229.5	17.4	7.0	19.0	Y	23
13. Blueberry	V	4.9	8.2	5.5	0.8	N	4
14. Bogbrook	F	21.0	3.7	8.2	95.0	Y	11
15. Bragonier	V	17.8	8.5	6.1	4.0	N	10
16. Butternut	F	522.9	12.8	7.8	40.0	Y	10
17. Camp	V	23.9	9.5	6.2	2.0	N	5
18. Clara	L	34.1	11.4	6.0	1.4	N	6
19. Clear	O	424.5	30.5	6.8	10.0	N	15
20. Clear	O	14.7	7.3	6.9	20.0	N	10
21. Clear	V	224.8	13.7	7.4	33.0	Y	28
22. Cloud	F	11.7	8.2	7.2	52.0	N	9
23. Crab	V	384.1	18.3	6.9	25.0	Y	16
24. Crescent	O	244.7	9.5	7.3	31.0	Y	17
25. Crystal	L	42.5	6.7	7.7	15.0	N	10
26. Crystal	V	36.4	21.0	5.9	8.0	N	6
27. Currie	O	39.0	4.3	5.6	0.3	N	10
28. Day	V	47.3	14.6	6.2	8.0	N	7
29. Dorothy	O	38.9	10.7	7.6	3.0	N	9
30. Dorothy Dunn	V	28.3	8.2	6.9	16.0	N	10
31. Echo	I	89.0	7.6	7.1	41.0	Y	19
32. Erickson	V	42.9	5.5	7.2	24.0	Y	13
33. Escanaba	V	116.6	7.6	7.3	25.0	Y	24
34. Flannery	O	45.3	10.6	5.7	0.3	N	11
35. Flora	V	41.3	9.2	6.0	8.0	Y	10
36. Forest	V	188.6	18.3	8.2	30.0	N	15
37. Fourmile	O	88.2	8.8	6.9	22.0	Y	23
38. Franklin	F	335.5	16.2	6.6	18.0	Y	12
39. Garth	O	46.2	6.7	7.5	38.0	N	14
40. George	O	176.0	7.9	6.4	22.0	Y	21
41. Gilmore	O	129.5	7.3	8.6	36.0	Y	28
42. Goodall	V	9.7	4.3	5.5	1.0	N	6
43. Gordan	F	21.9	9.8	5.7	2.0	N	7
44. Hilderbrand	L	24.2	8.0	5.1	0.2	N	8
45. Hixon	O	20.2	8.5	6.8	17.0	N	13
46. Homestead	V	8.9	5.2	5.2	0.5	N	4

APPENDIX: (*Concluded*).

Lake	County[a]	Area (ha)	Maximum depth (m)	pH	Alkalinity (mg/L as $CaCO_3$)	Tributary stream(s)[b]	Number of fish species
47. Horseshoe	L	6.2	10.7	5.8	4.0	N	7
48. Howell	F	71.6	4.6	8.0	64.0	Y	14
49. Ike Walton	V	582.4	19.2	5.6	0.4	N	8
50. Island-Round	O	179.5	7.9	6.3	19.0	Y	26
51. Island	V	414.0	10.7	7.4	37.0	Y	23
52. Johnson	V	9.7	3.7	7.2	23.0	Y	12
53. Kazmier	F	10.9	7.3	7.2	15.0	Y	7
54. Laura	F	44.5	6.4	6.2	2.0	N	7
55. Laura	V	242.4	13.1	7.9	32.0	N	13
56. Laurel	O	93.9	8.2	6.9	20.0	Y	24
57. Little Fork	O	143.3	10.4	6.9	22.0	Y	26
58. Little John	V	67.2	5.8	8.0	45.0	Y	22
59. Little Rock	V	14.6	7.5	6.3	1.0	N	7
70. Little Trout	V	397.4	27.8	7.1	20.0	N	14
61. Lower Ninemile	V	261.4	2.4	6.5	24.0	Y	16
62. Lucerne	F	407.0	22.3	6.9	22.0	Y	20
63. Ludington	F	12.1	9.5	5.8	5.0	N	5
64. Lumen	O	19.8	7.2	5.2	0	N	8
65. Manitowish	V	200.7	18.6	7.4	35.0	Y	27
66. Maple	V	19.0	4.3	6.0	5.0	N	7
67. Medicine	O	150.5	13.7	6.9	19.0	Y	25
68. Nelson	V	10.9	15.8	7.0	17.0	N	17
69. Norway Pine	I	12.1	5.0	6.8	9.0	N	7
70. Otter	F	32.8	4.3	7.9	88.0	Y	10
71. Owl	I	51.0	11.6	6.6	4.0	Y	15
72. Pallete	V	70.0	19.8	8.1	12.0	N	14
73. Pier	O	104.0	3.7	7.4	26.0	Y	13
74. Planting Ground	O	409.6	11.3	6.6	22.0	Y	22
75. Quartz	F	19.0	4.0	5.6	4.0	N	5
76. Rangeline	O	49.8	8.5	7.2	34.0	Y	19
77. Rest	V	255.6	14.9	7.4	37.0	Y	27
78. Richardson	F	19.0	3.7	8.9	86.0	Y	9
79. Round	F	27.1	3.1	9.2	70.0	Y	11
80. Sandy Beach	I	45.3	2.1	7.1	25.0	Y	12
81. Shannon	V	14.2	7.6	5.8	2.0	N	7
82. Silver	F	135.2	7.6	7.1	29.0	Y	14
83. Sparkling	V	51.4	19.5	7.8	38.0	N	16
84. Squash	O	158.6	24.9	7.3	18.0	N	10
85. Stevens	F	119.4	3.7	7.4	67.0	Y	15
86. Stormy	V	212.5	18.6	8.1	18.0	N	13
87. Tambling	V	68.4	3.4	7.2	35.0	Y	15
88. Thompson	O	154.6	10.7	6.4	23.0	Y	17
89. Toulish	V	32.0	11.0	6.7	20.0	N	14
90. Tower	V	10.1	8.5	7.4	18.0	N	7
91. Townline	O	61.5	5.8	6.9	36.0	Y	18
92. Trout	V	1566.0	35.1	7.6	27.0	Y	33
93. Vandercook	V	38.4	10.1	5.7	1.0	N	8
94. Wapoose	F	13.0	4.6	7.7	8.0	N	7
95. White Deer	F	25.1	7.0	6.9	1.0	N	4
96. Whitney	V	41.3	2.4	7.3	22.0	Y	8
97. Windfall	F	22.7	8.2	8.2	120.0	Y	13
98. Woodbury	F	29.1	6.1	6.8	3.0	N	7
99. Zottle	O	11.4	11.6	5.6	0.8	N	5
100. Unnamed 6−4	V	8.1	8.5	6.6	2.0	N	5

[a] County names: F, Forest; I, Iron; L, Lincoln; O, Oneida; V, Vilas.
[b] Inlet or outlet streams present: Y, yes; N, no.

Optimal Stock Size and Harvest Rate in Multistage Life History Models

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If the life history of a population consists of a sequence of density-dependent stages linked by density-independent survival rates, and if the density-dependent stages take the form of the Beverton–Holt stock and recruitment curve, then a single Beverton–Holt curve will describe the entire life history. The relationship between the parameters of any stage in the life history and the optimal harvest rate and optimal stock size is analyzed. Increasing survival rates will always increase the optimal harvest rate, but may increase or decrease the optimal stock size. Increasing the habitat capacity will increase the optimal stock size and leave the optimal harvest rate unaffected. An example of changing freshwater survival rates by Salmonid Enhancement is shown, as is an example of changing ocean survival rate. As we acquire a better understanding of the determinants of survival and habitat capacity, we should adjust harvest rates and stock size as the environment changes.

Si le cycle vital d'une population se compose d'une succession de stades dépendants de la densité liés par des taux de survie indépendants de la densité et si les premiers peuvent être décrits par une courbe de recrutement de Beverton–Holt, alors une seule courbe de Beverton–Holt pourra servir à la description complète du cycle vital. Les auteurs présentent la relation entre les paramètres de chaque stade du cycle vital, la taille optimale du stock ainsi que le taux optimal d'exploitation. Une augmentation des taux de survie entraînera toujours un accroissement du taux optimal d'exploitation mais pourra aussi accroître ou diminuer la taille optimale du stock. Par contre, une amélioration de la capacité de l'habitat amènera une augmentation de la taille optimale du stock mais ne touchera pas le taux optimal d'exploitation. Salmonid Enhancement présente un exemple de modification de taux de survie en eau douce et un exemple de modification de taux de survie en eau de mer. Suite à l'acquisition d'une meilleure compréhension des facteurs déterminants de la survie et de la capacité de l'habitat, les taux d'exploitation et la taille d'un stock seront peut-être ajustés en fonction des variations environnementales.

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The analysis of stock–recruitment data is widely used and accepted in fisheries theory and management (Parrish 1973). The stock–recruitment relationship can be used by itself to determine the optimal harvest rate or the optimal stock size when the species is semelparous, as in Pacific salmon (*Oncorhynchus* sp.), or can be combined with assumptions about growth and mortality (Deriso 1980). Variation of the stock–recruitment data is often ascribed to random environmental fluctuations (Walters and Hilborn 1976), and studies of the statistical structure of this variation have been performed (Peterman 1980). The assumption is always that there is a serially uncorrelated environmentally induced variation superimposed on an underlying relationship.

The assumption of a constant underlying curve is now being challenged on two fronts. First, many well-documented cases have emerged where the relationship between the environment and recruitment is understood, and the environmental effects are serially correlated. Oregon coho salmon (*O. kisutch*) production has been dropping in recent years, and may be explained by lagged upwelling (ODFW 1982; Clark and McCarl 1983). Upwelling occurs in the correlated runs of years. Similarly, Bristol Bay (Alaska) sockeye salmon (*O. nerka*) production depends upon spring weather conditions, times of ice breakup, and ocean temperature which is highly cyclic (Rogers 1980; Staty and Jaenicke 1980). If we can predict upwelling or temperature, and we know these affect stock and recruitment, should we change our harvest policy in light of this new information, and if so, how should we change it? Should the managers of Bristol Bay sockeye change their harvest rates or escapement goals if they believe that a series of poor survival years are upcoming due to low temperatures?

Anthropogenic effects can also modify the stock–recruitment relationship. Hydroelectric development on the Columbia River has increased downstream mortality and this will affect the stock–recruitment relationship. Does this affect the optimal escapement or the optimal harvest rate? Human activity such as stream improvement, flow regulation, or habitat modification will also affect the stock–recruitment relationship, and therefore optimal fishing policies.

In this paper we address the above questions and develop a life history stage by stage model of the stock–recruitment process based on the stock–recruitment model of Beverton and Holt (1957). Our intent is to show how survival rates and habitat capacity parameters of a number of life history stages can be combined into an aggregate stock–recruitment model. The optimal harvest rate and stock size for the aggregate model are derived as are the sensitivities of the harvest rate and stock size to changes in parameters at any intermediate life history stage. These calculations can provide a tool for management of populations whose intermediate life history stages are subject to varying effects.

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A Multistage Stock and Recruitment Model

Consider Beverton and Holt's stock–recruitment model written in the form

$$(1)\quad R = \frac{pS}{1 + \frac{p}{c}S}$$

where R = number of recruits, S = number of spawners, p = productivity parameter, and c = capacity parameter.

In a hypothetical population consisting of two stages, juveniles and adults, assume that the above functional form holds for both stages, but that the parameters are stage specific. Then

$$(2)\quad R_1 = \frac{p_1 S}{1 + \frac{p_1}{c_1}S}$$

represents the first stage, where R_1 = juveniles produced and S = spawning adults, and

$$(3)\quad R_2 = \frac{p_2 R_1}{1 + \frac{p_2}{c_2}R_1}$$

represents the second stage, where R_2 = adults produced and R_1 = juveniles from stage 1.

Substituting for R_1 we get

$$(4)\quad R_2 = \frac{p_1 p_2 S}{1 + \left(\frac{p_1}{c_1} + \frac{p_1 p_2}{c_2}\right) S}.$$

This may be repeated for more stages, and a general form for n stages may be represented by

$$(5)\quad R_n = \frac{p_1 p_2 \dots p_n S}{1 + \left(\frac{p_1}{c_1} + \frac{p_1 p_2}{c_2} + \dots + \frac{p_1 p_2 \dots p_n}{c_n}\right) S}.$$

This expression gives the recruitment of an n-stage production function at any stage in terms of the initial spawning stock and parameters describing productivity and capacity of intermediate stages up to and including the nth stage. In effect, equation (5) is a disaggregated form of the Beverton–Holt stock–recruitment relationship.

Now let

$$(6)\quad P_n = \prod_{i=1}^{n} p_i$$

be a composite of productivity parameters of n successive stages. This defines the overall productivity of a stock as a product of productivities of all intermediate stages. For example, the productivity of a given stock may be represented as the average fecundity multiplied by the product of survival rates through successive stages up to sexual maturity. Also let

$$(7)\quad C_n = \frac{P_n}{\sum_{i=1}^{n} \frac{P_i}{c_i}}$$

be a cumulative capacity parameter, expressed as a function of the composite productivity parameter P_n and the sum in the denominator of equation (5). Unlike the simple product in equation (6), the cumulative capacity C_n depends both on capacity and on productivity. Equation (5) may then be rewritten as

$$(8)\quad R_n = \frac{P_n S}{1 + \frac{P_n}{C_n}S}.$$

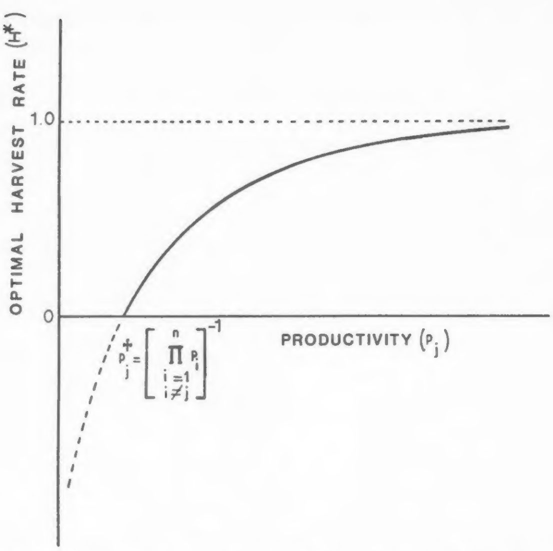

FIG. 1. Relationship between optimal harvest rate and productivity parameter p_j for any intermediate stage j in an n-stage stock and recruitment model corresponding to equation (15); $p_j^{\dagger}$ is the productivity threshold at which harvest rate becomes positive.

Having this general expression for a multistage stock–recruitment relationship, it is now feasible to examine the effect on management decisions of changes in intermediate parameters of productivity and capacity. We first derive an expression for optimum stock size and harvest rate from the general multistage form of the recruitment function. To do this we differentiate equation (8) with respect to S, set the derivative equal to one to maximize surplus over replacement, and solve for the optimal stock size S^*. Thus

$$(9)\quad \frac{\partial R}{\partial S} = \frac{P_n}{\left(1 + \frac{P_n}{C_n}S\right)^2} = 1$$

and therefore

$$(10)\quad S^* = \frac{C_n}{P_n}(P_n^{1/2} - 1).$$

The corresponding optimal recruitment is

$$(11)\quad R^* = \frac{P_n S^*}{1 + \frac{P_n}{C_n}S^*}$$

which may be simplified by substituting for S^* from equation (10) giving

$$(12)\quad R^* = S^* P_n^{1/2}.$$

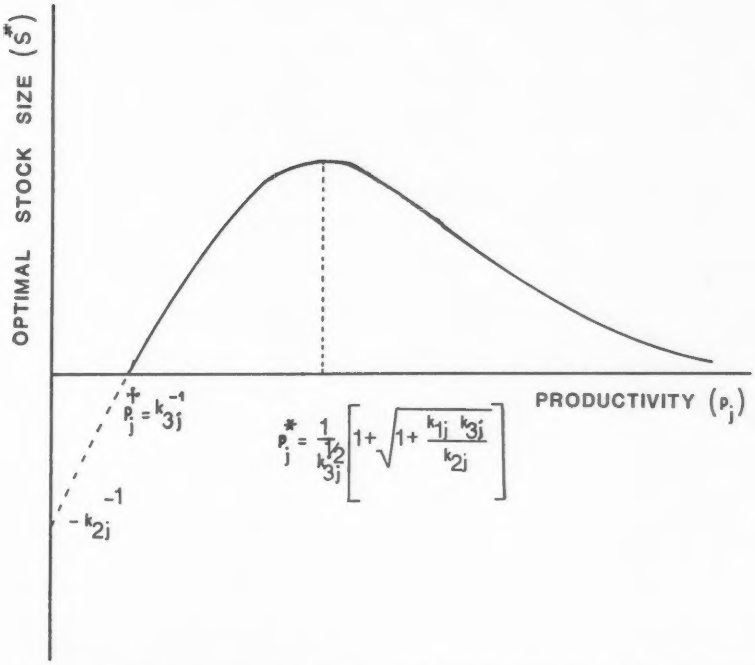

FIG. 2. Relationship between optimal stock size and productivity parameter p_j for any intermediate stage j in an n-stage stock and recruitment model corresponding to equation (16); $p_j^{\dagger}$ is the productivity threshold below which it is optimal to harvest the stock to extinction. The inflection point p_j^{*} is where the derivative of equation (10) equals zero and S^* reaches a maximum.

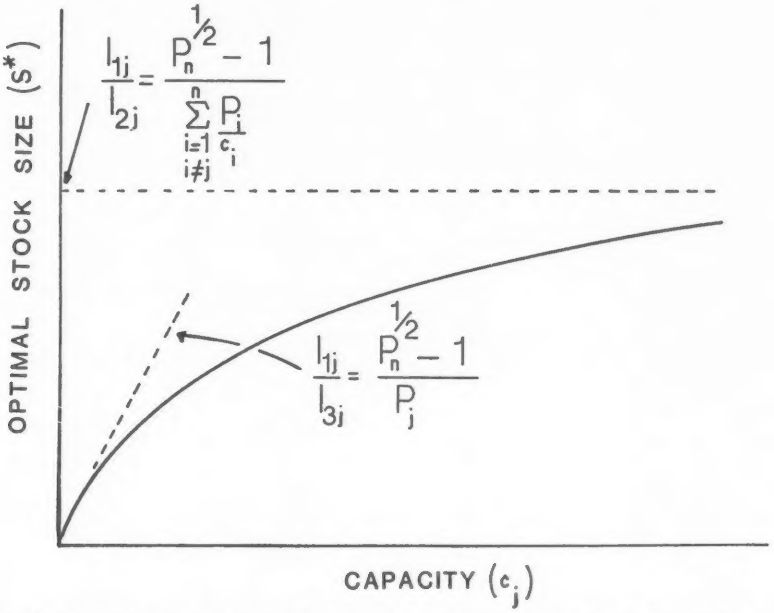

FIG. 3. Relationship between optimal stock size and capacity parameter c_j for any intermediate stage j in an n-stage stock and recruitment model corresponding to equation (17).

If the optimal harvest rate H^* is defined by

$$(13)\quad S^* = R^*(1 - H^*)$$

then

$$(14)\quad H^* = 1 - P_n^{-1/2}$$

which could be made an explicit function of any component p_j, as in

$$(15)\quad H^* = 1 - \left[\prod_{\substack{i=1 \\ i \neq j}}^{n} p_i\right]^{-1/2} p_j^{-1/2}.$$

This relationship is independent of capacity and is shown graphically in Fig. 1. Equation (15) implies that the only requirement for the management of a given stock by regulating the harvest rate is information on the productivity of this stock through its successive stages, regardless of stock size or capacity of these stages.

Equation (10) may be used to show explicitly the dependence of optimal stock size S^* on the parameters p_j and c_j which describe some intermediate jth stage ($2 \leq j \leq n$). (When $j = 1$ the problem is reduced to a single stage expressed in equation (1).) Thus

$$(16)\quad S^*_{(p_j)} = \frac{k_{3j}^{1/2} p_j^{1/2} - 1}{k_{1j} + k_{2j} p_j}$$

where

$$k_{1j} = \sum_{i=1}^{j-1} \frac{P_i}{c_i}$$

$$k_{2j} = \frac{1}{p_j} \sum_{i=j}^{n} \frac{P_i}{c_i}$$

$$k_{3j} = \frac{P_n}{p_j}$$

are independent of j, as one can see by using equation (6). This functional relationship between S^* and p_j is shown in Fig. 2 where, starting from some threshold $p_j^\dagger$, S^* increases with p_j up to p_j^*, and then decreases.

Likewise, it is possible to explicitly show the dependence of S^* on c_j for some stage j ($2 \leq j \leq n$). Thus

$$(17)\quad S^*_{(c_j)} = \frac{l_{1j} c_j}{l_{3j} + l_{2j} c_j}$$

where

$$l_{1j} = P_n^{1/2} - 1$$

$$l_{2j} = \sum_{\substack{i=1 \\ i \neq j}}^{n} \frac{P_i}{c_i}$$

$$l_{3j} = P_j.$$

Equation (17) has the familiar saturation type form shown in Fig. 3 with an initial slope of l_{1j}/l_{3j} and an asymptote of l_{1j}/l_{2j}.

We can also solve for P_n and C_n recursively such that the overall productivity and capacity parameters up to and including some stage n may be defined in terms of the $(n - 1)$th stage. This may be useful, particularly because we do not need to know details of preceding stages, only the overall parameters. Thus the ratio P_n/C_n in equation (8) may be expressed as

$$(18)\quad \frac{P_n}{C_n} = \frac{p_1}{c_1} + \frac{p_1 p_2}{c_2} + \ldots + \frac{p_1 p_2 \ldots p_n}{c_n}$$

$$(19)\quad = \frac{p_1}{c_1} + \frac{p_1 p_2}{c_2} + \ldots + \frac{p_1 p_2 \ldots p_{n-1}}{c_{n-1}} + \frac{p_1 p_2 \ldots p_{n-1} p_n}{c_n}$$

$$(20)\quad = \frac{P_{n-1}}{C_{n-1}} + \frac{P_{n-1} p_n}{c_n}.$$

However,

$$(21)\quad P_n = P_{n-1} p_n;$$

therefore, equation (20) may be rewritten as

$$(22)\quad \frac{P_{n-1} p_n}{C_n} = \frac{P_{n-1}}{C_{n-1}} + \frac{P_{n-1} p_n}{c_n}.$$

Dividing equation (22) by P_{n-1} gives

$$(23)\quad \frac{p_n}{C_n} = \frac{1}{C_{n-1}} + \frac{p_n}{c_n}$$

and the capacity parameter for any stage n may be expressed recursively as

$$(24)\quad c_n = \frac{c_n C_{n-1}}{\dfrac{c_n}{p_n} + C_{n-1}}.$$

This derivation allows us to write the stock–recruitment relationship recursively such that the new recruits to any stage may be expressed in terms of the composite parameters up to the $(n - 1)$th stage. Thus, when substitutions are made, the recursive form of equation (8) becomes

$$(25)\quad R_n = \frac{P_{n-1} p_n S}{1 + \left(\dfrac{P_{n-1} p_n}{C_{n-1} c_n}\right)\left(\dfrac{c_n}{p_n} + C_{n-1}\right) S}.$$

Discussion

Stock and recruitment models are useful tools for the management of exploited populations, particularly when mechanisms acting on intermediate life history stages cannot be predicted or controlled. The sum total of these mechanisms is compressed into two parameters, namely productivity of the stock and habitat capacity. However, these parameters are assumed constant from year to year; thus, stock and recruitment models do not allow the incorporation of expected changes in life history events. If mechanisms acting during life history events are elucidated, then it is possible to disaggregate the recruitment function into constituent components. Furthermore, the effect of these mechanisms on the harvest policies can be made explicit.

Factors governing marine growth and survival (Lasker 1975, 1978, 1979, 1981; Kruse and Tyler 1983; Kreutz et al. 1982) point to the potential use of physical measurements such as wind velocity (Lasker 1981; Bakun 1973, 1975) or nearshore temperature regimes (Kruse and Huyer 1983) to estimate conditions of survival. If marine survival of fish is coupled to specific oceanographic variables, albeit with a margin of uncertainty, then a life history model such as the one presented here may be a useful tool.

Although we are beginning to understand the factors that affect ocean survival rates (ODFW 1982; Clark and McCarl

1983), we do not yet know how to modify such rates. If early and critical ocean survival depends on the temporal pattern of upwelling, as interpreted by nearshore temperature structure, and if we observe that such a structure is changing, we could increase or decrease requisite escapement goals in response.

The implications of expected changes on management decisions are not readily obvious; indeed they may appear to be in conflict. For example, a fisherman with a short-time horizon would advocate higher catches before an expected prespawning mortality takes its toll. A regulatory agency, on the other hand, with a long-term mandate for the resource would recommend higher escapements to compensate for the higher expected prespawning mortality. Using a specific decision rule, namely to maximize the long-term harvestable surplus, the apparent conflict may be resolved by the explicit incorporation of expected changes in life history parameters, such as survival rates, into management decisions.

An interesting result of our analysis is the importance of habitat capacity when survival rates are being compared. If there is no habitat capacity constraint, then the optimal escapement goes up with higher rates of survival, but if the habitat capacity is limiting, then the optimal escapement goes down. This result, shown in Fig. 2, has management implications that are particularly relevant to human activities influencing survival rates. The ascending limb of the curve, bounded by $p_j^{\dagger}$ and p_j^{*}, represents a region where improvements in survival rates result in increasing optimal escapement. This may be explained by the increasing utilization of the habitat capacity at some intermediate stage. The maximum in Fig. 2 is due to the contribution of the constant k_{2j} in equation (16). Optimal stock size S^* would increase indefinitely if $k_{2j} = 0$, i.e. if all the capacities c_i were infinite. However, if any c_i is finite, then $k_{2j} > 0$, and S^* has a maximum.

To illustrate the relationships derived in the preceding section, we provide the following two examples. In both cases we utilize data that were not designed for the model itself; our purpose is to illustrate how our analysis can be used, not to make specific recommendations for the two examples.

Freshwater Limitation

The Salmonid Enhancement Program (SEP) in British Columbia employs a set of standard assumptions about the life history parameters in the analysis of alternative enhancement projects. These assumptions are called biostandards (SEP 1982), and are generally derived as averages from a large number of studies.

Table 1 presents an analysis of changing freshwater survival for coho salmon. Table 1(a) shows an analysis using the biostandards for a hypothetical stream with 10 000 m^2 of spawning and rearing habitat. The total productivity P_n is shown as 2.25, a very modest productivity due, primarily we believe, to the use of an average survival rate biostandard as the productivity from egg-to-smolt. Since the biostandard is derived from average egg-to-smolt survival rates from many studies, including some where density is high, this parameter will almost certainly underestimate the survival rate (productivity) when density-dependent effects are absent.

Table 1(b) shows the effect of increasing the egg-to-smolt survival rate; the optimal harvest rate increases, as does the optimal escapement. Table 1(c) shows the effect of increasing the egg-to-smolt survival rate still further, and now the optimal escapement decreases, but optimal harvest rate still rises. This shows how we have crossed over the highest point in Fig. 2, and any further increase in egg-to-smolt survival rates will lower the optimum escapement.

TABLE 1. Assumed productivities and capacities for coho salmon (*O. kisutch*) in a typical coastal British Columbia stream.

	Productivity (p_i)	Capacity (c_i)
(a) Assumed egg-to-smolt productivity		
Spawner-to-egg	1 250	2 500 000
Egg-to-smolt[a]	0.012	10 000
Smolt-to-adult	0.15	∞
Total	2.25	1 125
Optimum escapement = 250		
Optimum harvest rate = 0.33		
(b) Egg-to-smolt productivity doubled		
Spawner-to-egg	1 250	2 500 000
Egg-to-smolt	0.024	10 000
Smolt-to-adult	0.15	∞
Total	4.5	1 286
Optimum escapement = 320		
Optimum harvest rate = 0.53		
(c) Egg-to-smolt productivity increased further		
Spawner-to-egg	1 250	2 500 000
Egg-to-smolt	0.05	10 000
Smolt-to-adult	0.15	∞
Total	9.375	1 389
Optimum escapement = 305		
Optimum harvest rate = 0.67		

[a] 0.012 is almost certainly too low but is used for illustration.

Changing Marine Survival

Bristol Bay sockeye salmon constitute the single largest run of salmon in North America. These runs have shown drastic fluctuations that have been related to changing ocean temperatures and survival rates. The last 5–7 yr have produced excellent runs to Bristol Bay, but there is a concern that large-scale weather changes may result in lower temperatures and lower ocean survival in the near future. In the following example we provide an illustration of how a simple life history model for sockeye salmon could be constructed and utilized to determine management decisions in response to environmental changes. The data are estimates we have made from personal communication with Bristol Bay biologists and several unpublished reports. The purpose is illustrative, and the specific parameters do not necessarily constitute the current level of knowledge by biologists familiar with Bristol Bay.

Table 2(a) shows an analysis of the Kvichak River system in Bristol Bay. Using an estimate of very high ocean survival (0.20) we arrive at an optimum escapement of 15 135 000. Table 2(b) shows the effect of ocean survival being reduced to 0.05, the optimum escapement drops to 4 068 000. Clearly the

TABLE 2. Hypothetical analysis of optimum escapement and harvest rate for Kvichak River sockeye salmon (*O. nerka*).[a]

	Productivity (p_i)	Capacity (c_i)
(a) Good ocean survival		
Spawner-to-egg	1 000	∞
Egg-to-smolt	0.05	350 000
Smolt-to-adult	0.20	∞
Total	10.0	70 000
Optimum escapement = 15 135		
Optimum harvest rate = 0.68		
(b) Ocean survival reduced to 0.05		
Spawner-to-egg	1 000	∞
Egg-to-smolt	0.05	350 000
Smolt-to-adult	0.05	∞
Total	2.5	17 500
Optimum escapement = 4 068		
Optimum harvest rate = 0.37		

[a] All capacities and escapements are in thousands, thus the optimum escapement is 15 135 000 in case (a) and 4 068 000 in case (b).

optimum escapement and optimum harvest rate are very sensitive to the ocean survival rate, and if systematic changes in ocean survival rate can be expected, then management should respond with changes in escapement goals and harvest rates.

Productivity, Capacity, and Survival

Although the model we present is rather simple, one of its most useful purposes is to clarify the concepts of productivity and habitat capacity. We must distinguish between stocks that can produce many recruits per spawner (productive stocks) and stocks that can produce large recruitments simply by having large capacities. Many people use the term "productivity" to refer to the total size of a stock. We have used the term "productivity" to refer to the parameters relevant to the sustainable harvest rate and the term "capacity" to refer to parameters determining the action of density-dependent mechanisms. We recommend similar usage in future studies.

The optimum harvest rate depends only on the productivities, whereas the optimum escapement depends on both productivities and capacities. In our preceding discussion we have tended to assume that it is obvious whether changes would affect productivity or capacity. Increasing the spawning area or rearing habitat would presumably affect capacity, whereas predator removal, instream feeding, etc., would increase productivity. However, it is possible that instream feeding, for instance, might reduce the effective territory size and therefore increase capacity. We need to be very explicit in our consideration of how manipulations, intentional or otherwise, will affect the life history parameters.

Other Models

We have presented a single form of a multistage life history model, one based on the Beverton–Holt stock–recruitment curve. This particular model is convenient because it collapses the entire life history into a single equation. We have also investigated a number of other possible models, including ones using the Ricker stock–recruitment curve and those with connected straight-line segments. These do not produce the elegant analytic results, but do lead to similar conclusions. Since it is easy to numerically solve for the optimum escapement and harvest rate for any life history model (it can be done on a standard spreadsheet), researchers and managers should feel free to make any extensions or modifications to our model that are appropriate for their own situation.

Fisheries science has been dominated for the last 30 yr by the perspective of single-stock dynamics. The tools that have become widespread, surplus production, stock–recruitment, cohort analysis, and catch-at-age analysis, all assume that the external physical and biological conditions are random effects with no systematic change. As we become more sensitive to changes in the physical environment, and to the biological components of food, predators, and competitors, we need to develop tools to find management policies to deal with changing conditions. We have presented a first step by identifying the problem and analyzing a simple model. Specific analyses for detailed case studies are now needed.

Acknowledgments

We gratefully acknowledge Dr. C. J. Walters for showing us the recursive nature of the Beverton–Holt stock–recruitment curve. We also wish to thank Dr. T. L. Betlach, Dr. A. T. Charles, and an anonymous referee for their suggestions and comments. This work was supported in part by funds from the Salmonid Enhancement Program of the Department of Fisheries and Oceans.

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Body Fat Condition in Northeast Atlantic Fin Whales, *Balaenoptera physalus*, and Its Relationship with Reproduction and Food Resource

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Measurements of body girth, blubber thickness, and the lipid content of blubber, muscle, and visceral fat of Icelandic fin whales (*Balaenoptera physalus*) showed a consistent pattern of body fat condition for each sexual class in all years between 1977 and 1982, with pregnant and anoestrous females being fattest. There was a trend of increasing body fatness between 1977 and 1982 which is supported by data on oil production from the catch. Parallel to this was an apparent increase in food abundance and whale fecundity.

Les mesures qu'on a prises chez des rorquals communs (*Balaenoptera physalus*) d'Islande pour déterminer le diamètre de l'animal, l'épaisseur du panicule adipeux et sa teneur en lipides ainsi que le pourcentage de gras dans les muscles et les viscères ont montré qu'il y avait une tendance uniforme dans la teneur corporelle en gras pour chaque groupe sexuel à chaque année de 1977 à 1982, et que les femelles en gestation et en phase de repos étaient les individus les plus gras. La quantité de gras a eu tendance à augmenter entre 1977 et 1982, fait qui est appuyé par les données sur la production de l'huile tirée des prises. Parallèlement, il y a eu une augmentation sensible de la quantité de nourriture disponible et de la fécondité des baleines.

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An average catch of 242 fin whales (*Balaenoptera physalus*) has been taken annually off S.W. Iceland since 1948 (Lockyer 1981a). The season normally lasts through the summer months of June to September, when the whales are feeding locally on swarming euphausiids, notably *Meganyctiphanes norvegica*.

North Atlantic fin whales are generally believed to exhibit the same migratory and breeding habits as their Southern Hemisphere counterparts (Lockyer and Brown 1981; Lockyer 1984; Lockyer et al. 1977; Martin 1982) which have an annual migration towards polar waters in summer for feeding, and towards more subtropical and temperate waters in winter for breeding. The basic reproductive cycle is a 2-yr one comprising 11 mo of gestation (with conception and birth taking place in midwinter) followed by 7 mo of lactation so that the calf is weaned on the feeding grounds in the summer following birth. Whereas Brodie (1975, 1978) and Mitchell (1974) observed that coastal northwest Atlantic fin whales off Nova Scotia, of which some possibly originate from Newfoundland, may be locally resident and feeding for most of the year, I am considering a different fin whale stock on the eastern side of the north Atlantic for which I am assuming some seasonal behaviour.

The catch is biased by International Whaling Commission (IWC) regulations (IWC 1950, 1983) which impose a minimum size on the catch of 50 ft (15.2 m), and prohibit the take of calves and any adult accompanying a calf (i.e. a lactating female). In addition, in the Icelandic fishery, the belly is cut open at sea to cool the body, which usually results in loss of fetuses and, frequently, damage to the reproductive organs. This practice influences the measurements of girth, and the detection of pregnancy.

An increase in body fatness throughout the feeding season has been shown for Southern Hemisphere fin whales, especially pregnant females (Lockyer 1978, 1981b, 1981c). Further, the difference in fatness between pregnant and lactating females supported calculations of the energy drain during reproduction, mainly due to the costs of lactation. For Icelandic fin whales, the extra cost of reproduction above that required for maintenance would be 23–32% for adult females, depending on age, over the 2-yr cycle. On an annual basis, the extra food energy required for pregnancy and lactation (assuming 80% assimilation efficiency) would thus represent 16–23% and 29–41% of total intake, respectively. The costs of reproduction are energetically expensive and the underwriting fat reserves must be laid down during the summer feeding period. Presumably the rate of deposition and the total deposit are affected by food availability.

My objective is to demonstrate that in addition to variation in body fatness between individuals of different reproductive status (Lockyer et al. 1985), year to year variations occur, which can be linked with food resource and ultimately with fecundity.

Materials and Methods

Fin whale tissues were collected for total lipid content analysis in 1978 and 1981 during the period July–August at the coastal Icelandic whaling station, Hvalur H.F. Blubber and muscle were sampled from the posterior dorsal position (determined as most suitable for indicating body fat condition by Lockyer et al. 1985). Blubber was collected as described in Lockyer et al. (1984), with about 100 g of the attached underlying muscle. About 100 g each of visceral fat from the cardiac and intestinal regions, liver, and kidney was also sampled. All tissues, once sampled, were deep frozen and maintained at −26°C. Postmortem times ranged from approximately 13 to 26 h.

Lipid extraction was by the method of Bligh and Dyer (1959) using chloroform−methanol, as described by Lockyer et al. (1984). Muscle, visceral fat, and the visceral organ tissues were homogenised from 0.5- to 1.0-g pieces of frozen tissue cut from the innermost parts of the samples (to minimise effects of autolysis and volatile lipid loss). All lipid contents are expressed as percent lipid weight per wet weight tissue.

Anatomical measurements on length, girth, and blubber thickness were also made. Blubber thicknesses were mainly taken in situ, at the same site as the tissue samples. Body girth was determined by measuring half-girth, while the whale lay on one side on the flensing plan, from approximately the mid-length position assessed as most sensitive for detecting changes due to fattening (Lockyer et al. 1985). Two main problems existed here: some body shape distortion occurred from the whale resting on a hard surface, and occasionally, parts of the carcase protruded through flensing cuts. Both factors, especially the latter, caused the girth to be overestimated by 5−8% (Lockyer et al. 1985), and girths collected when extensive flensing cuts were present were not used for analysis. Body length from jaw tip to tail fluke notch, measured in a straight line, was also recorded for each whale.

Complementary data collected by or on behalf of the Sea Mammal Research Unit (SMRU), Cambridge, were available on blubber thickness measured from one standard position on the posterior flank of every whale caught each season from 1977 to 1982 inclusive during June−September inclusive. Factory production data on oil yield for the 1977 to 1982 seasons (years of comparable data) were kindly made available by Hvalur H.F. These data covered periods of 14−17 wk from the end of May to early October, and included total rorqual oil production for both fin and sei whales combined.

Data collected by or on behalf of SMRU on presence of a corpus luteum in the ovaries of mature females taken between June and September each season, 1976 to 1982, were available. The presence of an active corpus luteum was taken to indicate a likely pregnancy, and certain ovulation. Absence of a corpus luteum but presence of corpora albicantia was indicative of the mature anestrous condition.

Data on euphausiid abundance were supplied by the Institute of Marine Environmental Research (Natural Environment Research Council) in Plymouth, England, from the continuous plankton recorder (CPR) system, collected during 1971−82. The system operates with plankton recorders being towed by merchant ships and Ocean weather ships along standard routes at monthly intervals throughout each year. The plankton recorders are towed at a standard 10-m depth with an aperture 12.5 mm^2. Filtration operates through a slowly moving band (bolting cloth, 24 meshes$\cdot cm^{-1}$), held in place by a second band, at a rate of 100 mm$\cdot$10 mL of tow^{-1}, when 3 m^3 of seawater is filtered off into a storage spool of formalin. The collected samples are sorted and analysed according to the data processing system described by Colebrook (1975). The CPR system has been operational for over 45 yr and represents a unique time-tested long-term record of plankton availability in the north Atlantic. Data analysed here were from samples collected in the region bounded by 59−63°N and 31−43°W in the Denmark Strait, representing part of, but an unknown proportion of, the feeding area for the Icelandic whales. Data from the months July−September were selected for analysis, these representing the relevant summer period for which a complete monthly series of samples existed for all the years. The euphausiid abundance data were pooled for the entire period 1971−82 and a mean value ±SD obtained. Each season's estimate of abundance was then represented in units of standard deviation of the mean for the 12-yr period to gauge relative seasonal abundance over this time span.

Data on stomach contents of Icelandic fin whales caught in 1977−82 inclusive, collected and examined by or on behalf of SMRU, were also available for analysis of feeding activity. Data from June to September each year were combined and analysed for proportion of empty stomachs and food type.

Results and Discussion

Anatomical Measurements

Data and analyses on body length, girth, and blubber thickness have been presented by Lockyer et al. (1985). They concluded that significant differences existed between the reproductive classes, with adult females, usually the pregnant ones, being thickest in girth and in blubber thickness, followed by sexually mature males, immature females, and, thinnest, immature males. The whales in 1981 had significantly thicker blubber than those examined in 1978. Despite significantly smaller body lengths for all sexual classes in 1981 compared with 1978, and significantly thicker girths for all sexual classes in 1981 compared with 1978, a comparison of the body length − girth regressions for each year indicated that the two slopes were significantly different, with 1981 whales thicker regardless of length. The concomitant increase in blubber thickness, however, is not sufficient to account for the massive girth increase in 1981. This latter increase may be attributable to body fat being deposited elsewhere, presumably in muscle and in and around visceral organs.

Biochemical Analyses — Lipid Content of Body Tissues

The variation in mean lipid content in blubber, muscle, liver, and visceral fats is given in Table 1. The blubber lipid content does not appear to vary significantly between reproductive classes within a season, but 1981 shows a 30% increase over 1978 ($p < 0.01$, two-way ANOVA). The muscle lipid content shows more variability between classes, although 1981 is again higher for most individual classes. The juvenile males have least lipid, followed by immature females. The mature pregnant and anestrous females have most. A two-way ANOVA (Table 1) indicates that the seasonal difference is also highly significant for muscle ($p < 0.01$), and although there is no significant difference between reproductive classes for blubber, in the muscle there is a highly significant difference between reproductive classes when adult males are excluded ($p < 0.01$). The single lactating female in each season has lowest blubber lipid content of all whales.

Neither liver nor visceral fats appear to vary between classes (Table 1). There is limited sampling in 1981 although for individual classes, the visceral fat in 1981 may be increased in lipid content over 1978.

TABLE 1. Mean ± SE lipid content (expressed as percentage of wet weight) of body tissues of Icelandic fin whales.

		Posterior dorsal blubber		Posterior dorsal muscle		Liver		Visceral fats		Sample size	
Sex	Sexual condition	1978	1981	1978	1981	1978	1981	1978	1981	1978	1981
M	Imature	53.2±7.9	70.6±1.5	7.8±4.3	12.4±1.6	3.2±0.7	Nil	57.5±5.7	Nil	3	5
M	Mature	52.7±11.6	72.5±2.4	15.6±6.4	11.5±1.3	3.6±0.7	Nil	50.5	62.1±8.6	4	5
F	Immature	58.5±9.1	71.0±1.2	15.8±2.8	21.2±0.7	3.5±0.4	Nil	54.2±12.7	Nil	3	6
F	Mature, anoestrous	65.5±0.3	76.8	21.6±10.1	29.3	5.2±3.0	Nil	63.8±12.2	Nil	3	1
F	Mature, pregnant	45.0±6.4	75.1±3.3	18.8±4.0	26.0±1.9	3.5±0.7	Nil	64.0±4.7	73.5	6	3
F	Mature, lactating[a]	39.4	59.0	17.6	18.5	3.3	2.8	62.8	79.3	1	1

NOTE: Two-way ANOVA. Blubber: sex ($p > 0.05$, v.r. = 1.31, df = 4/4), season ($p < 0.01$, v.r. = 29.52, df = 1/4); muscle (adult males excluded): sex ($p < 0.01$, v.r. = 81.83, df = 3/3), season ($p < 0.01$, v.r. = 71.76, df = 1/3).

[a] Excluded from analysis.

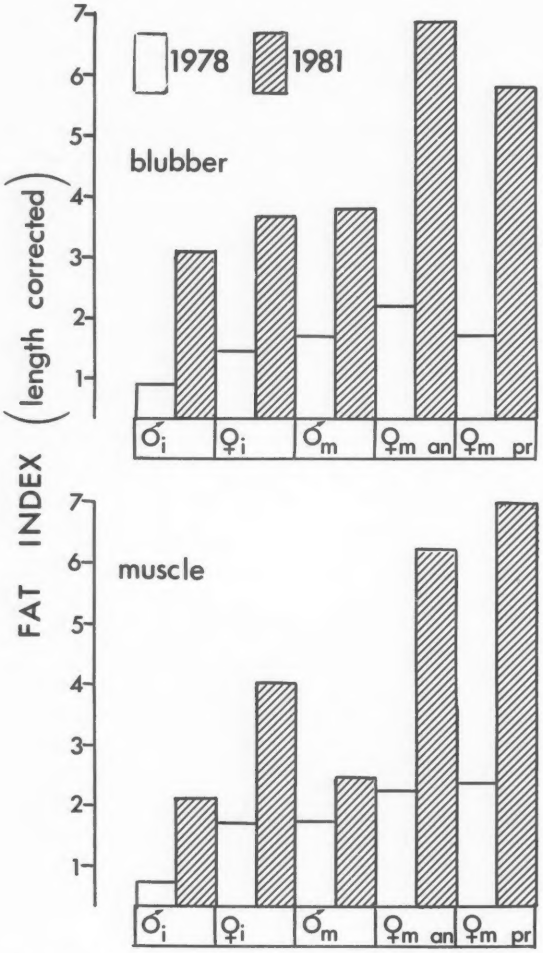

FIG. 1. Body fat condition in fin whales expressed on a relative basis for 1978 and 1981 by reproductive class. i = immature; m = mature; an = anoestrous; pr = pregnant.

Body Condition Assessed as a "Fat Index"

The anatomical and biochemical data demonstrate that all whales were significantly fatter in the 1981 season compared with the 1978 season. There is also an indication that pregnant and anoestrous females are fatter than other reproductive classes.

No actual weight data for tissues are available so that I have attempted to integrate the data on fat condition results in a measure of "fat index" defined as follows.

(1) Blubber: Mean body girth × mean blubber thickness × percentage lipid content of blubber

(2) Muscle: Mean cross-sectional area of the body inside the blubber layer × percentage lipid content of muscle.

Because of differences in body length between the classes of animals, and the length–girth correlation, the fat indices have been adjusted to a standard body length. This adjustment changes the basic results insignificantly between the seasons of 1978 and 1981 by 0.8–5.1% and does not alter the fatness pattern between reproductive classes. The length-adjusted fat indices are shown in Fig. 1.

The differences in body fat condition between 1978 and 1981 are clearly evident, and the relative fatness of mature females is very marked in 1981. In 1981, the muscle as well as blubber is notable as a fat store in females.

Some questions still remain regarding actual differences in fatness both between seasons and between individual reproductive classes. Despite sampling periods in both 1978 and 1981, individual reproductive classes may, by analogy with the Southern Hemisphere stocks (Lockyer and Brown 1981), arrive at different times during the season, so that whilst precise information is unavailable for Icelandic fin whales, one might expect the fatness of pregnant females to be exaggerated relative to other classes because of a slightly earlier arrival on the feeding grounds (Lockyer 1981b). Similarly, juveniles frequently arrive later than adults, so that again the fatness of adults might be overemphasised. Consequently it is possible that these data are slightly biased.

Independent Assessment of Fatness

An attempt to examine the fattening process both over the entire summer season and over several years was made by

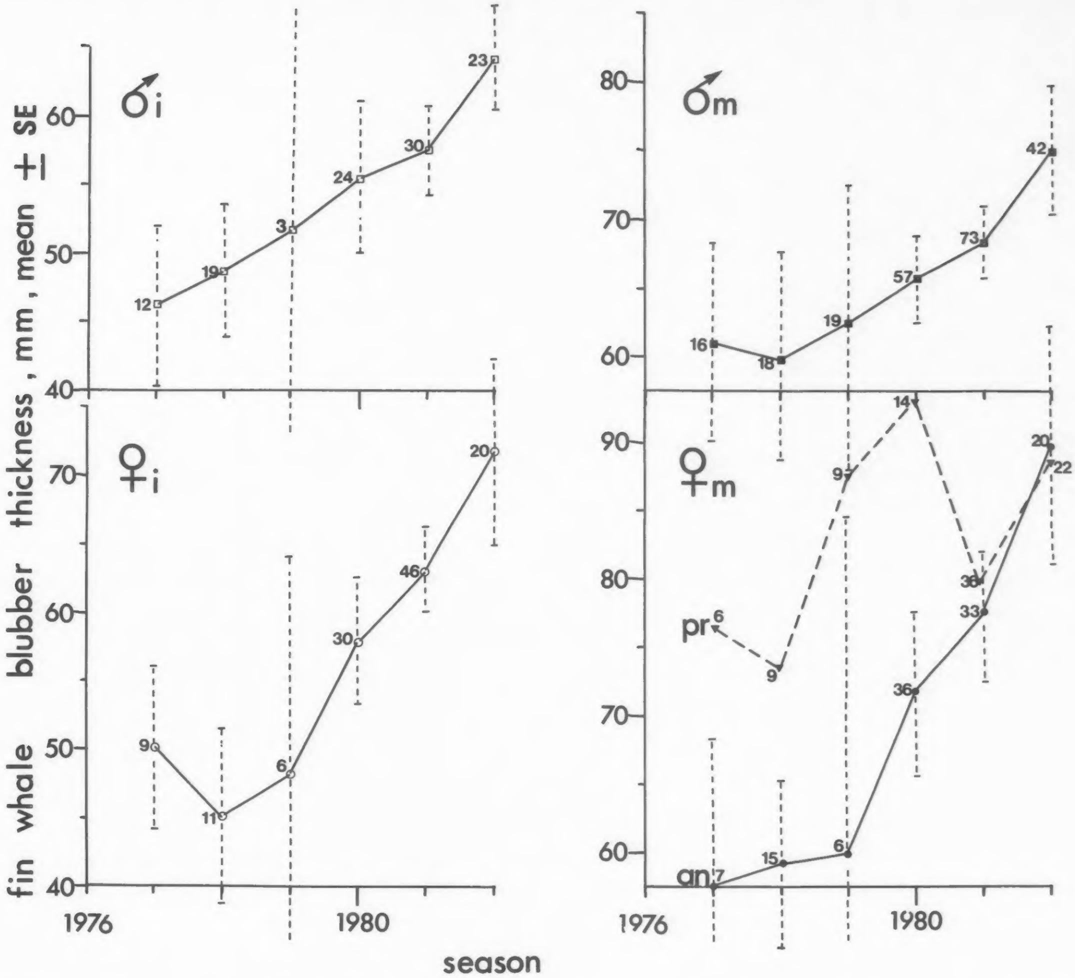

FIG. 2. Blubber thickness on the dorsal flank in fin whales during 1976−82 by reproductive class. i = immature; m = mature; an = anoestrous; pr = pregnant. Sample size is given beside each mean value.

analysing independently collected data on blubber thickness and oil production from the same Icelandic stock of fin whales during the period 1977−82 inclusive.

Figure 2 shows mean blubber thickness by reproductive class. The means (±SE) indicate an increase in fatness between 1977 and 1982, complementary to the results given for 1978 and 1981. Again, pregnant females are the fattest animals.

The whaling company oil production figures were adjusted to allow for the variable proportion of sei whales (*Balaenoptera borealis*) in the catches by assuming an equivalent of (a) two sei and (b) three sei to each fin whale, based on the old Blue Whale Unit (Mackintosh 1965). Despite variations in sex ratio and size of whales of both species, different peak catching periods, and variability in meat quality each season resulting in changes in the ratio of frozen meat to oil production, all factors complicating the utilisation of the data, there is an increasing trend with year (Fig. 3), supporting the data on body fatness. Between 1978 and 1981 inclusive, a regression coefficient of 0.567 is significant at $p < 0.05$ ($t = 4.462$, df = 2).

These data on blubber thickness and oil yield therefore indicate that there has been an overall improvement in whale body fat condition between 1978 and 1981. They also confirm differences in fatness between reproductive classes.

Food Supply

An increase in body fat should be correlated with an increase in the available food. To test this relationship, I examined the data on stomach fill and euphausiid abundance.

The percentage of empty stomachs has declined between 1978 and 1981, and conversely the percentage containing food items, regardless of quantity, has increased (Fig. 4). The difference in stomach fill between 1977 and 1982 inclusive is highly significant, using a χ^2-test ($p < 0.001$, $\chi^2 = 45.95$, df = 4). Most seasons do not provide details on food quantity in a standard way, so that more elaborate analysis of stomach fill is not meaningful. Of all stomachs examined during 1977−81 inclusive, the euphausiid *M. norvegica* comprised 93.8−100% of the diet; no association of diet component and year was

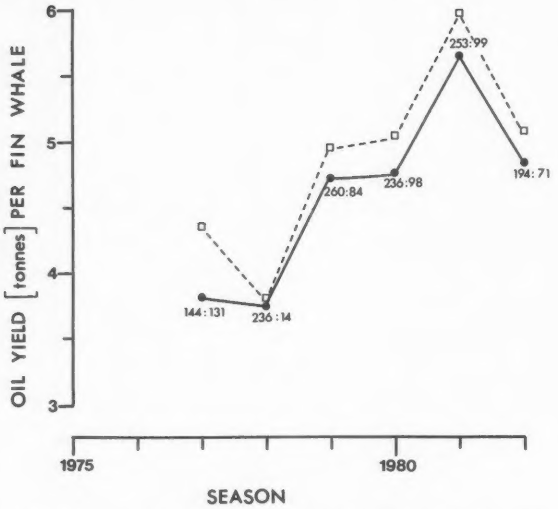

FIG. 3. Calculated oil yield per fin whale from factory oil production, 1977–82, at Hvalur H.F., Iceland. Fin whale to sei whale catch ratio: ●, 1 fin = 2 sei; □, 1 fin = 3 sei.

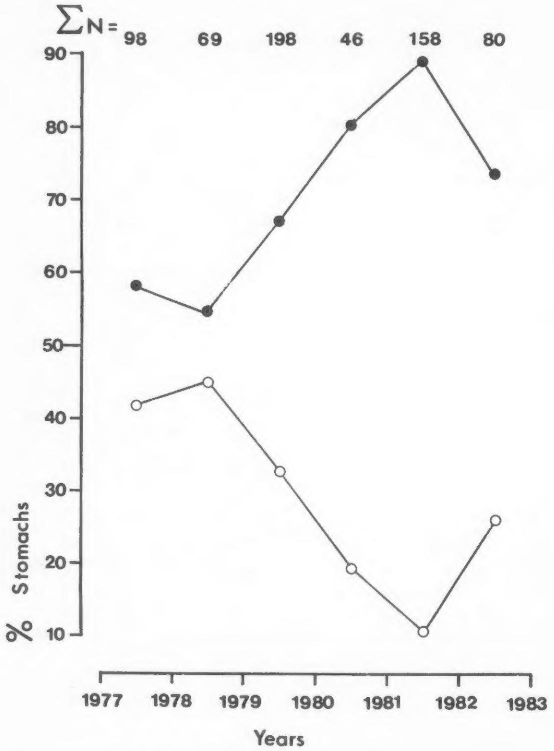

FIG. 4. Stomach fill of fin whales examined June–September inclusive during 1977–82 inclusive. ○, empty; ●, containing food.

found. Other food items included capelin (*Mallotus villosus*) and squid identifiable only from beaks or flesh. I conclude, therefore, from Fig. 4, that between 1978 and 1981, fin whales were increasingly successful in obtaining food.

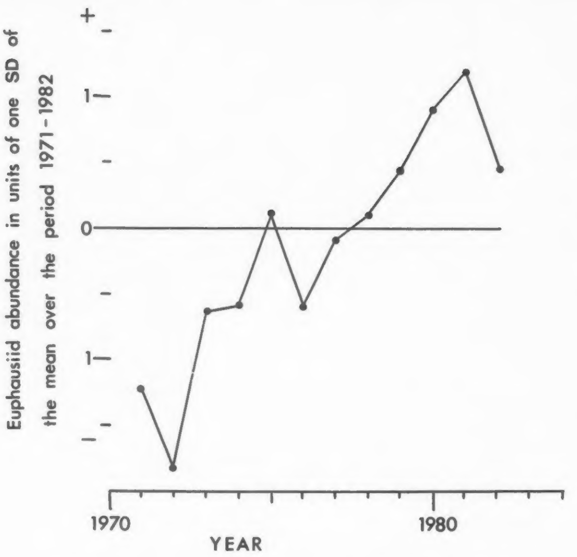

FIG. 5. Relative abundance of euphausiids in waters off S.W. Iceland during July–September in area bounded by 59–63°N and 31–43°W. Data by courtesy of IMER, Natural Environment Research Council, England.

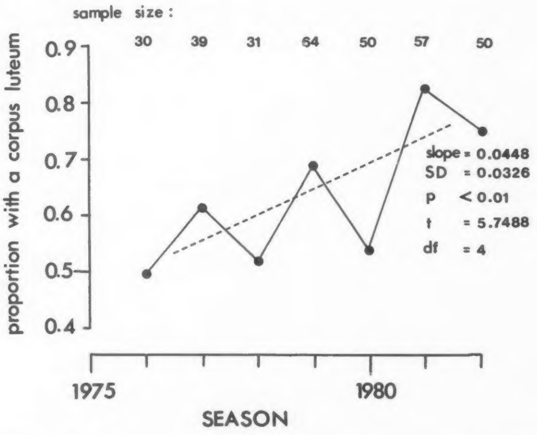

FIG. 6. Relative fecundity of female fin whales by season, 1976–82, gauged from the proportion of nonlactating females with a corpus luteum in the mature female catch.

Euphausiid abundance in the Denmark Strait (Fig. 5) appears to have been increasing between 1972 and 1981 with a crossover point from below to above average between 1975 and 1978, the upward trend between 1978 and 1981 being significant ($p < 0.01$, $t = 15.929$, df = 2), with a regression coefficient of 0.374. This trend appears to be reflected in the increasing body fatness during this period.

Absolute abundance of food may be affected by environmental factors (for example, water temperature, currents affecting productivity). Thus, investigating the annual abundance of prey from plankton recording during the feeding season of the whales may only be a weak indicator of actual availability of food to the whales. In 1981, however, ships reported that the sea areas of the whaling grounds during July appeared pink from the profuse swarms of krill.

Another obvious criticism of using a general euphausiid abundance as an indication of food supply is that whales consume mainly swarming euphausiids of a particular size, the predominant food species being *M. norvegica*, although fin whales are known for their opportunistic feeding behaviour (Kawamura 1980). The size of euphausiid consumed in 1977 was frequently recorded as a small larval form, different from the larger form normally observed in later years of sampling.

Ovulatory Activity as a Measure of Potential Fecundity

Figure 6 shows the proportion of nonlactating mature females in the catch, with a corpus luteum present in the ovaries, for each season from 1976 to 1982 inclusive. Despite an apparent 2-yr oscillation, there is an upward trend, and 1981 shows a large increase in proportion over 1978. Calculating a regression on the running means to dampen the oscillations, the slope of the linear regression, 0.0448, is significant at $p < 0.01$ ($t = 5.7488$, df = 4). It thus appears that there has been an increase in potential fertility in females over this time period.

Theoretical Prediction of Interdependence between Food Supply, Fat Storage, and Fecundity

Over a short period of consecutive seasons off Iceland, food supply, body fat condition, and fecundity have all increased significantly. The conclusion therefore is that improved body fat condition resulting from increased food resource may be the cause of increased ovulation rate.

I have calculated (Lockyer 1978, 1981b, 1981c) that the energy drain of the reproductive cycle, especially lactation, is considerable to the female. Production of a viable calf probably depends on the success of the summer feeding for adequate fat storage to cover these reproductive costs, because of the seasonal variations in the pattern of feeding.

The relative fatness of pregnant females observed here, compared with other classes, may be the result of energy storage necessary to meet such reproductive energy drain. Presumably, if feeding conditions and consequentially fat storage are poor in any one season, the female has few options: she may fail to ovulate, or fail to conceive, or fail to suckle the calf should pregnancy go to term; alternatively, the basic reserves normally required for maintenance may be preferentially chanelled into reproduction in order to carry a fetus and to complete lactation. This latter alternative might prolong the period of anoestrus and hence the reproductive interval while the female rebuilds her energy reserves — a situation that should be apparent in the proportion in the catch of ovulating females (females with a corpus luteum), assuming most such females become pregnant. Conversely, it may be speculated that the 2-yr cycle could be reduced in years of high food availability, the ultimate time-limiting factor being the length of gestation.

While variations in body fatness cannot yet be translated into actual quantitative energy reserves for individual whales because blubber fat, muscle, and internal organs were not weighed, future studies will investigate intraseason variation in body fatness, covering the entire summer feeding period, and will monitor the interrelationship of body fatness, food supply, and fecundity.

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Light and Nutrient Effects on the Relative Biomass of Blue-Green Algae in Lake Phytoplankton

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The factors determining the relative biomass of blue-green algae during the growing season were studied using data from 22 lakes worldwide. Multiple linear regression analyses suggest that total nitrogen (TN), total phosphorus (TP), and light (as estimated from Secchi disc transparency and the depth of the mixed layer) interact to determine the relative biomass of planktonic blue-green algae. At a fixed TN:TP ratio, blue-green relative biomass increases as light availability decreases. At a fixed light level, blue-green relative biomass also increases as the TN:TP ratio decreases. Both effects are consistent with current knowledge of algal physiology, and with a recently proposed theoretical framework for algal community structure.

On a étudié les facteurs qui déterminent la biomasse relative des algues bleues au cours de la période de prolifération à l'aide de données obtenues dans 22 lacs du monde entier. Des analyses de régression linéaire multiple donnent à penser que l'azote total (NT), le phosphore total (PT) et la lumière (telle qu'évaluée à partir de la transparence observée avec le disque de Secchi et de la profondeur de la couche de mélange) interagissent pour déterminer la biomasse relative des algues bleues planctoniques. Pour un rapport constant NT:PT, la biomasse relative des algues bleues augmente lorsque la lumière disponible diminue. À un niveau constant d'intensité lumineuse, la biomasse relative des algues bleues augmente également lorsque le rapport NT:PT diminue. Les deux effets sont en accord avec les connaissances que nous avons de la physiologie des algues et avec la théorie proposée récemment concernant la structure des communautés d'algues.

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During the past two decades, research on the factors controlling the biomass and photosynthetic activity of the phytoplankton (e.g. Sakamoto 1966; Dillon and Rigler 1974; Schindler 1978; Smith 1979; Ryding 1981; Vollenweider and Kerekes 1982) has greatly increased our understanding of primary production. However, our understanding of how this primary production is translated into phytoplankton community structure has lagged far behind. Clear differences exist in algal species composition, both between lakes and within a single lake over time, but the relative importance of competition (Tilman et al. 1982) and purely physical processes (e.g. Haffner et al. 1980) to these differences is not yet known.

Phytoplankton community structure has been a focus of study for many decades (Pearsall 1932; Hutchinson 1957; Rosén 1981), and numerous investigators have used algal species composition to characterize lake trophic state (e.g. Järnefelt 1952; Rawson 1956; Hörnström 1981; Rott 1984). However, specific algal taxa are associated with problems in water supply management, and it would be of practical value to be able to predict the conditions which favor (or select against) the dominance of these taxa. For example, the nuisance growth of blue-green algae (Cyanobacteria) is one aspect of eutrophication which is recognized as a major water quality problem worldwide (Reynolds and Walsby 1975; Horne 1979; Gregor and Rast 1980). If we can determine the ecological factors which lead to the dominance of blue-greens in lakes, we might then be able to develop rational water management strategies which would minimize their occurrence.

As noted by Reynolds and Walsby (1975) and Horne (1979), numerous factors may be involved in the ecological success of blue-greens. One proposed explanation for their dominance is that low nitrogen to phosphorus (N:P) ratios in the nutrient supply favor vacuolate, nitrogen-fixing blue-greens over other types of phytoplankton (Schindler 1977; Flett et al. 1980). Assuming that *all* blue-greens are good competitors for N, I extended Schindler's (1977) reasoning to include both nitrogen-fixing and non-nitrogen-fixing species, and tested this modified hypothesis using data from 17 lakes located worldwide (Smith 1983a, 1983b). In lakes having epilimnetic total nitrogen to total phosphorus (TN:TP) ratios greater than about 29:1 by weight, the proportion of blue-green algae tended to be less than 10% of the total phytoplankton biomass. However, at ratios <29, no clear pattern was evident, indicating that the N:P ratio hypothesis alone was insufficient to explain the dominance of blue-greens in lakes, and that other factors must be involved.

Data from other studies suggest that the underwater light climate is another important factor. For example, blue-green dominance has been observed in Lake Gjersjøen, Norway (Faafeng and Nilssen 1981), and in Thomson Lake, Ontario (Shindler et al. 1980), despite epilimnetic TN:TP ratios $\gg 29$ by weight. Dominance by blue-green algae in these lakes is more consistent with the conclusions of Mur et al. (1978), who suggested that low light availability in the water column favors the growth of blue-greens over other algal groups. It is likely then that light and nutrients both act to regulate the phytoplankton species composition (Gibson and Fitzsimons 1982; Zevenboom et al. 1982), but an extensive test of this hypothesis has not yet been made. The purpose of this paper is thus to explore the influence of light availability, N, and P on the relative biomass of blue-green algae, using data from a broad range of lakes.

Materials and Methods

Models for blue-green relative biomass were derived from data found in 22 sources. These included three limnocorrals in the Bay of Quinte, Lake Ontario (Liao and Lean 1978; Lean et al. 1978); five segments of Saginaw Bay, Lake Huron (Smith et al. 1977; Bierman and Dolan 1980; V. J. Bierman, Jr., U.S. EPA, Narragansett, RI, pers. comm.); Heart Lake (Ontario) (Nalewajko et al. 1981); Lake Trummen (Sweden) (Björk 1979; Cronberg 1982); and Lake Södra Bergundasjön (Sweden) (Leonardson and Bengtsson 1978), as cited in Smith (1985). Additional data were from Lake Washington, Loch Leven, Norrviken, Ontario, Vänern, Vättern, Mälaren (four bays), Hjälmaren, Michigan, George (Uganda), and Kinneret (Israel), as cited in Smith (1983a). Other data sources were Slapy Reservoir (Javornický 1966; Javornický and Komárková 1973; Procházková et al. 1973), Uttran (Forsberg 1978), Langvatn (Reinertsen 1982), Östra and Västra Ringsjön (Ryding 1983), and Tahoe (Goldman 1977).[1]

When estimates of blue-green relative biomass were not explicitly given in the data source, for each lake I estimated the mean total phytoplankton cell volume (TOTAL, cubic millimetres per cubic metre) in the epilimnion during each growing season (typically May–September). In addition, I estimated the mean total blue-green cell volume (BG) and the mean heterocystous (NFIX) and nonheterocystous (NONFIX) blue-green cell volumes when these data were available. All cell volume estimates were then coverted to algal biomass, assuming that 10^3 $mm^3 \cdot m^{-3}$ was equivalent to 1 g wet $wt \cdot m^{-3}$. The influence of the rarely counted picoplankton (Craig 1984; Caron et al. 1985) on the biomass estimates is not known.

In addition to algal biomass or relative biomass measurements, I obtained data for the mean depth (Z, metres), mean epilimnetic TN and TP concentrations (milligrams per cubic metre), and mean Secchi disc transparency (SD, metres) for the 20 lakes during each growing season. The mean depth of the mixed layer (Z_m) was estimated from thermal profiles in stratified lakes, unless given explicitly in the data source. In unstratified or briefly stratified lakes, the mixed depth was assumed to be equal to the mean depth. Estimates for the mixed depths of Vänern, Vättern, and Blacken (Lake Mälaren) are from Ramberg (1979), and estimates of the mixed depths of the five Saginaw Bay segments are from V. J. Bierman, Jr. (pers. comm.).

Statistical analyses of the data were made using the SYSTAT statistical software for the IBM PC (Wilkinson 1985). When several years' data were available for a single lake, each year was treated as a separate case; similarly, each limnocorral was treated as a separate case. A base 10 logit transformation (cf. Berkson 1953) of all relative biomass data was necessary to insure homosecedasticity and linearity during regression analyses. For example:

$$(1)\quad \text{logit}\ (\%\text{BG}) = \log\ (\%\text{BG}/(100 - \%\text{BG})).$$

Thus, in all analyses, the relative biomass data were expressed as a percentage. To reduce statistical bias from seven cases where the proportion of blue-green algae was either 0 or 100%, these values were set to 1 and 99%, respectively.

A statistical cross-validation procedure was also used when confirmation of the empirical models was desired, using a Turbo Pascal program written for the IBM PC by S. Case (Department of Biology, University of North Carolina, Chapel Hill, NC), and based on a Basic program by Y. C. Prairie (McGill University, Montreal, Que.). In this method, for a data set having *n* cases, $n - 1$ cases are used to calibrate the model and the remaining case is used to confirm the model. This procedure is then reiterated *n* times, with replacement, so that each case in the data set is used once as the confirming case (cf. Reckhow and Chapra 1983). The root mean square error of prediction (root PREMSE) derived from this analysis can be used to determine the prediction error for application of the model (cf. Smith 1985).

Results and Discussion

Effects of Light and Nutrients on the Relative Biomass of Blue-Green Algae

As emphasized by Reynolds and Walsby (1975) and by Van Liere and Mur (1980), SD and Z_m together provide a convenient estimate of the average light intensity in the water column. The use of TN, TP, SD, and Z_m in a stepwise multiple regression analysis of the entire data set suggested the following relationships (Table 1):

$$(2)\quad \text{logit}\ (\%\text{BG}) = 2.358 - 1.297 \log \text{TN} + 0.692 \log \text{TP} - 2.058 \log \text{SD} + 0.538 \log Z_m,\ r^2 = 0.52$$

$$(3)\quad \text{logit}\ (\%\text{BG}) = 1.096 - 1.604 \log \text{TN:TP} - 1.119 \times \log \text{SD}:Z_m,\ r^2 = 0.42.$$

Equations 2 and 3 and the validation analysis (Table 2) confirm that N, P, and light interact to determine the relative biomass of planktonic blue-green algae. The nature of this interaction can be illustrated graphically for a hypothetical lake having an average mixed depth of 10 m. I first predicted the mean summer concentrations of chlorophyll *a* from a series of values for TN and TP, using the multivariate model of Smith (1982):

$$(4)\quad \log \text{Chl}\ a = 0.653 \log \text{TP} + 0.548 \log \text{TN} - 1.517.$$

I then predicted the mean summer Secchi disc transparency from Chl *a* using the model of Carlson (1977):

$$(5)\quad \ln \text{SD} = 2.04 - 0.68 \ln \text{Chl}\ a$$

and calculated the expected proportion of blue-green algae for each case from Eq. 2. Consistent with the conclusions of Schindler (1977) and Smith (1983a, 1983b), Fig. 1 predicts that the proportion of blue-greens is sensitive to the TN:TP ratio. At a fixed transparency (SD), the %BG is reduced if the epilimnetic TN:TP ratio is increased. However, if the TN:TP ratio is held constant, an increase in transparency also results in a reduction in the proportion of blue-greens (Fig. 1).

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[1] A complete set of the tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

TABLE 1. Results of multiple regression analysis of data for blue-green relative biomass.

					Analysis of variance				
Variable	Coefficient	SE	T	P(2-tailed)	Source	SS	df	MS	F
A. Dependent variable: logit (%BG), N = 107									
Constant	2.358	1.009	2.34	0.021					
log TN	−1.297	0.408	−3.18	0.002	log TN	3.681	1	3.681	10.121
log TP	0.692	0.308	2.25	0.027	log TP	1.840	1	1.840	5.058
log SD	−2.058	0.400	−5.14	0.000	log SD	9.612	1	9.612	26.427
log Z_m	0.538	0.271	1.99	0.050	log Z_m	1.435	1	1.435	3.947
B. Dependent variable: logit (%BG), N = 107									
Constant	1.096	0.389	2.82	0.006					
log TN:TP	−1.604	0.254	−6.30	0.000	log TN:TP	17.092	1	17.092	39.723
log SD:Z_m	−1.119	0.239	−4.68	0.000	log SD:Z_m	9.408	1	9.408	21.864

TABLE 2. Results of cross-validation analysis of Eq. 2 and 3 (see text).

Source	df	SS	MS	F
A. Dependent variable: logit (%BG), N = 107				
Model	4	40.411	10.103	27.777
Residual	102	37.098	0.364	
Total (corr.)	106	77.510		
Root MSE	0.603	$R^2 = 0.521$		
Dep. mean	−0.162			
C.V.	−322.606			
Root PREMSE	0.630			
B. Dependent variable: logit (%BG), N = 107				
Model	2	32.761	16.380	38.069
Residual	104	44.749	0.430	
Total (corr.)	106	77.510		
Root MSE	0.656	$R^2 = 0.423$		
Dep. mean	−0.162			
C.V.	−261.532			
Root PREMSE	0.675			

Theoretical Considerations

The above evidence for control of blue-green relative biomass by the TN:TP ratio and light availability is consistent with recent suggestions that resource-based competition is a major factor structuring phytoplankton communities (Tilman 1982; Tilman et al. 1982). With regard to N and P, the optimum cellular N:P ratio is one factor which determines the outcome of algal competition (Rhee 1978; Tilman 1982; Smith 1983b). This ratio, Δ, is the point at which a transition from N to P limitation occurs, and can be calculated as the ratio of the subsistence quotas for N and P (Rhee 1980). If two (or more) species compete for N and P, it can be shown that differences in their optimal N:P ratios in part determine the conditions under which the species can coexist, and the conditions under which competitive dominance occurs (Tilman 1982).

However, it is clear from this analysis that light is also important, but the mechanism by which light influences blue-green relative biomass is not yet clear. Blue-greens possess several strategies by which they can outcompete other species under conditions of low light availability (Zevenboom and Mur 1984). In general, the Cyanobacteria appear to have lower light requirements than other taxa (cf. Richardson et al. 1983; however, also see Van Liere and Walsby 1982). In addition, buoyancy mechanisms allow many blue-greens to regulate their position in the underwater light field, and to overcome vertical separations between light and nutrient availability (Ganf and Oliver 1982; Oliver and Walsby 1984; Robarts and Zohary 1984).

In addition to the direct effects of light discussed above, an effect of light on competition for N and P is also probable. Zevenboom et al. (1980a, 1980b) and Rhee and Gotham (1981) have found a pronounced influence of light on the N subsistence quota, but the subsistence quota for P seems to be less light sensitive (Zevenboom et al. 1980b). These studies suggest that the optimal N:P ratio is light dependent, and that the value of this ratio should *increase* as light availability decreases. Such a light dependence of Δ has recently been confirmed by Healey (1985), and has important ecological implications. If light availability is decreased (either by increased algal biomass or by inorganic turbidity), the resulting increase in Δ should also increase the TN:TP ratio at which blue-green algae are competitively favored. This prediction is consistent with the trends suggested by Fig. 1 and suggests a possible mechanism for the observed nutrient–light interaction. Furthermore, the nonlinear relationship observed between light and the optimal N:P ratio (Healey 1985) may account in part for the nonlinear responses of blue-green relative biomass to light which are implied by Eq. 2.

Potential Effects of Zooplankton Grazing

In addition to competition, zooplankton grazing has also been proposed as an important factor influencing algal community structure (Porter 1977; Shapiro 1980). The framework presented in Fig. 1 may help explain the effects of zooplankton on blue-green relative biomass which were observed in Lake Trummen, Sweden, in 1970 (Björk 1979), and in Severson Lake, Minnesota, in 1965 (Schindler and Comita 1972). Following a winter fishkill in Lake Trummen in 1969, a subsequent pulse of large *Daphnia* appeared, and was followed by a dramatic reduction in total algal biomass during summer 1970. The summer mean transparency increased fourfold over previous years (Björk 1979; Shapiro 1980), and despite TN:TP

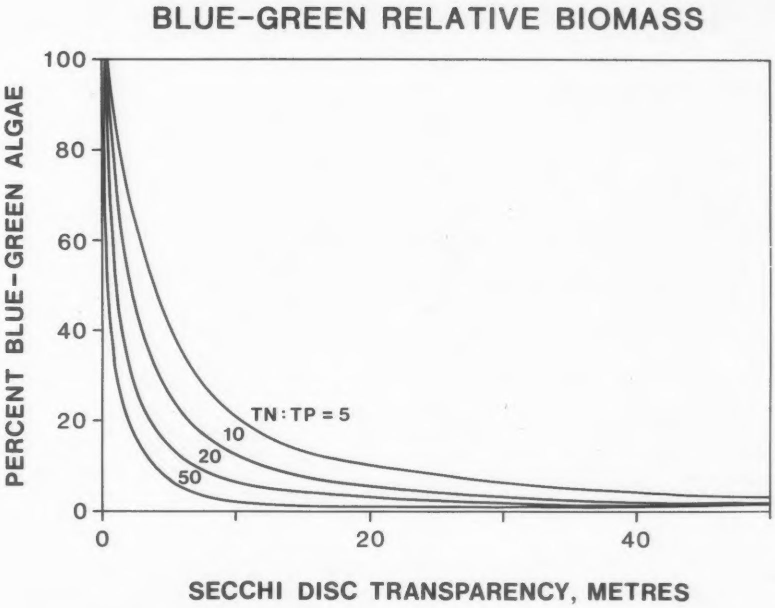

FIG. 1. Graphical presentation of the predictions of Eq. 2 for a hypothetical lake with a mixed depth of 10 m, demonstrating the effects of light availability (SD:Z_m ratio) and the TN:TP ratio on the relative biomass of blue-green algae. Note: this figure is for the purpose of illustration, not prediction.

ratios <10, blue-greens were not dominant in the lake (cf. Smith 1983a, fig. 1). Similarly, a winter 1964 fishkill in Severson Lake resulted in a shift from small herbivores to large *Daphnia pulex*, and subsequently to a more than fourfold reduction in summer algal biomass (Schindler and Comita 1972). The Secchi disc transparency was greatly increased, and a shift in dominance from blue-greens to green algae, chrysophytes, and euglenophytes occurred in summer 1965.

In both of the above lakes, and in the case of Indian Lake, Wisconsin (Lathrop 1983), it appears likely that the reduced success of blue-green algae was linked to increases in light availability which followed the appearance of large-bodied *Daphnia* spp. This hypothesis is consistent with recent experimental work by Carlson and Schoenberg (1983), and with the trends suggested by Fig. 1. However, in other cases the presence of large *Daphnia* is associated with blooms of *Aphanizomenon flos-aquae* (cf. Hrbáček 1964; Lynch 1980; Ganf 1983), and it would be of value to understand the factors which are responsible for the dominance of blue-greens in such systems.

Conclusions

It is clear from the analysis (Eq. 2 and 3) that N, P, and light influence phytoplankton community structure. However, it is not possible to distinguish the effects of light on competition for N and P from the more direct effects of light on algal growth rates. Although Van Liere and Walsby (1982) concluded that it is not possible to make generalizations about the growth responses of Cyanobacteria to light, a recent review by Richardson et al. (1983) suggested that the blue-greens tend to have lower light requirements for growth than other algal groups. If Richardson et al. (1983) are correct, then blue-greens may be favored under light-limiting conditions as proposed by Mur et al. (1978). Furthermore, low light levels enhance the buoyancy of many blue-greens, and would lead to a faster net growth rate in the water column by decreasing their sinking losses (van Rijn and Shilo 1983; Oliver and Walsby 1984). Conversely, high light levels may lead to a loss in cell buoyancy (Oliver and Walsby 1984), to photoinhibition of growth (Richardson et al. 1983), or to photooxidative death of Cyanobacteria (Van Liere and Walsby 1982). High light levels thus may act directly to reduce blue-green growth. The relative importance of these direct and indirect effects of light can only be assessed using experimental manipulations of light, N, and P in the laboratory and in situ.

It is also clear that N, P, and light account for only about half of the total variance observed in the 22 lakes studied (Eq. 2 and 3). A portion of this residual error stems from the fact that individual phytoplankton counts are typically associated with large relative errors (Willén 1976; Rott 1981), but substantial errors may also result from methodological differences among the original investigators (Table 1). However, despite the acknowledged limitations of the data set, this analysis has provided the first general models for blue-green relative biomass. The statistical tools used here can also be used to explore the effects of other variables such as carbon availability (Shapiro 1973) and zooplankton species composition (Carlson and Schoenberg 1983), and I hope that these techniques will be used to develop models for other major taxonomic groups as well.

Future research would thus benefit from more consistent methodologies, and it is of particular importance that new data be collected with hypothesis testing in mind. For example, the apparent importance of Z_m suggests that this variable should be more consistently reported, and that consistent quantitative criteria (e.g. Ganf and Oliver 1982; Reynolds et al. 1984) should be used to define the depth of the mixed layer. Furthermore, estimates of the effective underwater light climate (Ramberg 1979) should best be made in the future from direct light measurements with an underwater quantum sensor, rather than Secchi disc measurements (cf. Edmondson 1980; Megard et al. 1980). Finally, it is important that the mixed layer phytoplankton samples be taken using consistent sampling methods, preferably with an integrating tube sampler.

In addition to contributing to our understanding of the ecology of the Cyanobacteria, this analysis has important practical implications. The manipulation of influent N : P ratios has been used successfully to control the dominance of blue-green algae in lakes and ponds (Barica et al. 1980; Leonardson and Ripl 1980; Lathrop 1983; J. G. Stockner, Department of Fisheries and Oceans, West Vancouver, B.C. unpubl.). However, the models presented here suggest that management of influent N : P ratios alone in many cases will be insufficient. Equations 2 and 3 suggest the hypothesis that minimizing TP loading (to minimize chlorophyll-related light attenuation) and managing loading N : P ratios to obtain high TN : TP ratios in the lake may both be necessary if one's objective is to minimize the relative biomass of blue-green algae.

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Recent Major Declines in Zooplankton Populations in the Inshore Region of Lake Michigan: Probable Causes and Implications[1]

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Evans, M. S. 1986. Recent major declines in zooplankton populations in the inshore region of Lake Michigan: probable causes and implications. Can. J. Fish. Aquat. Sci. 43: 154–159.

Summer zooplankton communities in the inshore region of southeastern Lake Michigan were dominated by small species during the 1970s, suggesting that size-selective fish predation pressures were intense. Abundances of alewife (*Alosa pseudoharengus*), the dominant planktivore in the 1970s, declined in recent years, especially over 1982–84. Despite decreased alewife predation, small zooplankton taxa continued to predominate. Moreover, zooplankton standing stocks declined 10-fold during 1982–84, suggesting that predatory pressures had intensified. Concurrent with the alewife population decrease was a major increase in yellow perch (*Perca flavescens*) abundances. As a probable consequence of intense predation pressures exerted by abundant yellow perch, zooplankton standing stocks were severely reduced. Yellow perch populations may have been adversely affected by food limitation, especially in summer 1984 when zooplankton standing stocks were only 3% of their average level over 1975–81.

Les communautés zooplanctoniques observées en été près des rives de la partie sud-est du lac Michigan ont été dominées au cours des années 1970 par une espèce de petite taille, ce qui donne à penser qu'il y a une forte prédation par les poissons en fonction de la taille de ces organismes. Le nombre de gaspareaux (*Alosa pseudoharengus*), planctonivore le plus important dans les années 70, a diminué au cours des dernières années, particulièrement entre 1982 et 1984. Malgré une prédation moins grande de la part des gaspareaux, les groupes d'organismes zooplanctoniques de petite taille sont demeurés les plus nombreux. De plus, la biomasse du zooplancton a diminué de 10 fois entre 1982 et 1984, ce qui laisse supposer que le taux de prédation a augmenté. En même temps que la population de gaspareaux baissait, il y avait augmentation importante du nombre de perchaudes (*Perca flavescens*). À la suite probablement du taux élevé de prédation exercé par un grand nombre de perchaudes, la biomasse du zooplancton a diminué considérablement. La limitation de la nourriture disponible pourrait avoir nui aux populations de perchaudes, surtout au cours de l'été 1984, lorsque la biomasse du zooplancton se situait à seulement 3 % du niveau moyen atteint au cours de la période de 1975 à 1981.

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Since the early 1960s, the dominant planktivore in Lake Michigan has been the alewife (*Alosa pseudoharengus*). Alewife selectively consume the largest zooplankton, resulting in a shift in zooplankton community structure toward a greater dominance of small species (Brooks and Dodson 1965; Wells 1970; Warshaw 1972).

Lake Michigan alewife populations declined markedly over the late 1970s and early 1980s (Wells and Hatch 1984; Jude and Tesar 1985; Evans and Jude 1986). This provided an opportunity to investigate the relationship between fluctuations in alewife abundance and zooplankton community structure, comparing the inshore and offshore regions of Lake Michigan. My previous work (Evans et al. 1980) has shown that zooplankton community structure varies as a function of distance from shore (or station depth). These gradients are especially sharp during summer when the inshore region serves as a nursery area for several species of fish including alewife and yellow perch (*Perca flavescens*). At these times, the inshore region zooplankton community is dominated by small taxa (Hawkins and Evans 1979; Evans et al. 1980).

Previous Lake Michigan studies have documented the effects of fluctuations in alewife abundance on summer zooplankton community structure (Wells 1970). These studies were conducted in 1950s and mid-1960s in the offshore region. More recently, I observed that as alewife abundances declined over the late 1970s and early 1980s, the summer offshore zooplankton community changed in structure as larger *Daphnia* spp. increased in abundance (Evans 1985; Evans and Jude 1986). I anticipated that, in the inshore region, larger zooplankton would also increase in abundance as alewife populations declined. Furthermore, because the inshore zooplankton community appeared to be especially affected by alewife predation, I anticipated that shifts in zooplankton community structure would be at least as large as those observed in the offshore region. This was not observed either for *Daphnia* spp. (Evans and Jude 1986) nor for the other components of the zooplankton community.

Here I present the long-term trends (1972–84) in summer zooplankton community structure in the inshore region of southeastern Lake Michigan. I then describe the relationship between zooplankton populations (abundance, composition) and the recently observed changes in summer 1972–82 planktivorous fish abundances in the inshore region, as presented in

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Evans and Jude (1986), and autumn data (1983, 1984), presented by Wells and Hatch (1984) and L. Wells U.S. Fish and Wildlife Service, Ann Arbor, MI. pers. comm.).

Materials and Methods

The inshore region of southeastern Lake Michigan is defined as that area bounded by the 5- to 10-m depth contours (Evans et al. 1980). This region of the lake was sampled intensively from 1972 to early 1982 as part of a long-term monitoring study of the Donald C. Cook Nuclear Plant; limited sampling was conducted in later years. Detailed information on the zooplankton aspects of this study is provided in Evans et al. (1982, 1985). Data collected during July−August 1972−84 form the basis of this paper.

Zooplankton were collected from two locations in the inshore region. Between 1972 and May 1982 (when zooplankton monitoring studies were completed), zooplankton samples were collected during monthly lake survey cruises. Two vertical hauls were made from 1 m off the bottom to the surface using a 50-cm-diameter, 156-μm-mesh net equipped with a calibrated flowmeter. Seven (August) to 13 (July) stations were sampled along a band of water extending 11 km north and south of the plant site. Beginning in 1975, zooplankton samples also were collected monthly from the intake forebay of the Donald C. Cook Nuclear Power Plant located near Bridgman, Michigan. Cooling water is drawn through three intake pipes located at approximately the 7.3-m depth contour. Previous studies have shown that the intake provides a representative sampling location for investigation of long-term trends in zooplankton populations in the inshore region (Evans and Flath 1984).

Between 1975 and May 1982, two 5-min replicate pumped samples were collected from the intake at sunset, midnight, sunrise, and noon. Similar intake samples were collected through 1982 by D. Jude (Great Lakes Research Division, The University of Michigan) as part of a continuing (until December 1982) fisheries study. Some additional intake samples were collected in July and August 1983 and July 1984 by D. White (Great Lakes Research Division, The University of Michigan). Three consecutive 8-h collections were made from the intake forebay: one of these 8-h samples was examined from each collection date. In August 1984, two 5-min samples were collected at noon.

Samples were collected with a diaphragm pump which discharged water into a 30-cm-diameter, 156-μm-mesh net suspended in a barrel of water. The barrel was equipped with a flowmeter which allowed quantitative samples to be collected. Approximately 1 m^3 of water was filtered during a 5-min collection period. Samples were preserved with a sugar−formalin or 70% ethanol solution.

In the laboratory, each sample was divided in a Folsom plankton splitter to give two subsamples of several hundred organisms. At least one subsample was examined from each collection. For additional information on collecting and laboratory methods see Evans and Flath (1984).

Average summer zooplankton abundance was based on the mean July−August abundance. Similarly, for each taxon, average percent composition was based on the mean July−August percent composition. Calculations based on July−August means compensated, to some extent, for large seasonal variations in taxa abundances. Zooplankton biomass was estimated based on the numerical abundances of the various zooplankton taxa and their mean dry weights as reported in Hawkins and Evans (1979). Mean individual dry weight was estimated by dividing the mean total zooplankton standing stock biomass (milligrams per cubic metre) by mean zooplankton abundance (number per cubic metre).

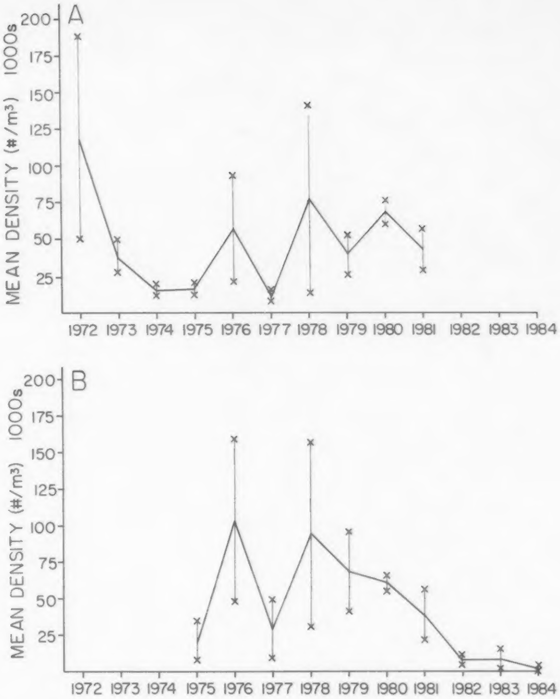

FIG. 1. Mean summer (July−August average) abundance of zooplankton in the (A) inshore region over 1972−81 and (B) intake waters of the Donald C. Cook Nuclear Plant over 1975−84. Also shown is the range in abundance, i.e. mean July and August abundances.

Results

Over summers of 1972−81, mean (July−August average) zooplankton abundances as determined by net hauls ranged from 11 977/m^3 (1977) to 119 095/m^3 (1972) and averaged 49 265/m^3 (± 33 462/m^3) (Fig. 1A). There was no obvious time trend to these data. Intake data, collected within a matter of days of inshore region data, followed a pattern similar to the inshore region data over 1975−81 (Fig. 1B). Mean summer (July−August average) intake abundances ranged from 21 165/m^3 (1975) to 105 541/m^3 (1976) and averaged 60 271/m^3 (± 31 901/m^3) versus a mean of 45 647/m^3 (± 25 453/m^3) for the inshore region during the same period.

After 1981, summer zooplankton samples were collected only from power plant intake waters. In 1982, mean summer zooplankton abundances were lower (7318/m^3) than during any of the previous 10 summers (Fig. 1). Abundances were similarly low in summer 1983 (8445/m^3) and then declined further to 1938/m^3 in 1984. Mean summer zooplankton abundance for 1982−84 was 5900/m^3 (±3477/m^3) or approximately 10% of the mean abundance for 1975−81 as determined by intake sampling.

Biomass data followed a trend similar to average summer

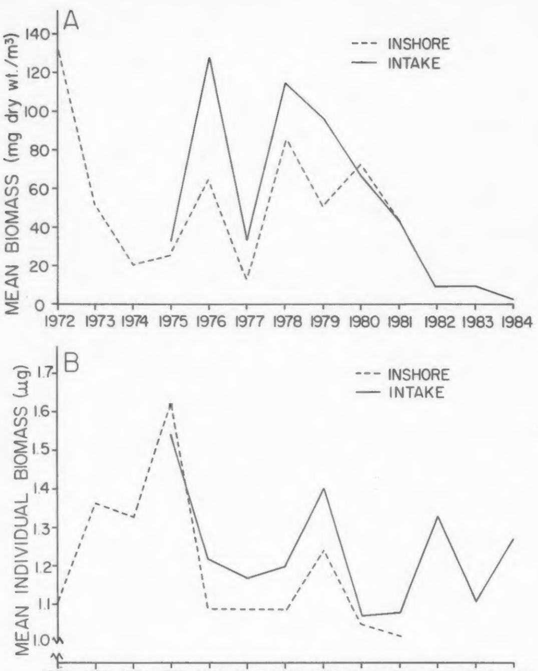

FIG. 2. Estimated (A) mean summer (July–August average) biomass of zooplankton in the inshore region (1972–81) and intake waters (1975–84) and (B) mean individual dry weight of zooplankton in inshore and intake waters over the same periods. See text for further explanation.

abundance data (Fig. 2A). Estimated mean summer biomass in the inshore region ranged from 13.04 mg/m^3 (1977) to 132.65 mg/m^3 (1972), averaging 56.41 mg/m^3 (±35.38) over 1972–81 and 51.19 mg/m^3 (±25.91) over 1975–81. In intake waters, estimated mean biomass over summer 1975–81 ranged from 32.55 mg/m^3 (1975) to 114.24 mg/m^3 (1978) and averaged 73.73 mg/m^3 (±39.92). Estimated mean biomass decreased over summer 1982–84, averaging only 7.17 mg/m^3 (±4.10) or 10% of earlier values. In summer 1982, estimated mean biomass averaged 2.45 mg/m^3 or 3% of the mean value over 1975–81 in intake waters. The estimated mean size of zooplankton was small, averaging 1.17 µg (±0.21) for collections made from the inshore region and 1.24 µg (±0.17) for collections made in the intake over summer 1975–81. Although zooplankton biomass (milligrams per cubic metre) decreased over 1982–84, there was no significant change in the estimated mean biomass (1.24 ± 0.11 µg) of zooplankters collected in intake waters.

Crustacean zooplankton community structure in the inshore region was similar during 1972–74 and 1975–81. For the purpose of economy, only the 1975–81 inshore region (vertical net hauls) and 1975–84 intake data are presented (Table 1). Most taxa occurred in similar abundances in intake and inshore region waters. Of the abundant taxa, only immature *Cyclops* spp. copepodites occurred in substantially higher abundances (greater than a factor of 2) in intake waters than in the vertical haul net collections made in the inshore region.

The most striking feature of zooplankton community structure during 1975–81 was the dominance of small zooplankters (Fig. 2B; Table 1). The most abundant taxon was the cladoceran *Bosmina longirostris*, a relatively small species. The next most abundant taxa also were small, and included nauplii, immature *Cyclops* spp. copepodites, and immature *Diaptomus* spp. copepodites. Large taxa, such as adult copepods and *Daphnia galeata mendotae*, occurred in relatively low numbers.

Crustacean zooplankton community structure differed only slightly between 1975–81 and 1982–84 (Table 1). Thus, during 1975–81, *Bosmina longirostris*, the dominant taxon, accounted for an average of 65.0% (intake collections) of the crustacean zooplankton and 58.5% during 1982–84. Most other taxa also occurred in similar proportions during the two time periods. Only *Chydorus sphaericus*, a very small cladoceran, and *Polyphemus pediculus*, a small predaceous cladoceran, occurred in substantially greater proportions over 1982–84.

Abundances of most taxa during summer 1982–84 were approximately 10% of their abundances over 1975–81 (Table 1). However, larger zooplankters such as *Diaptomus ashlandi*, *Diaptomus oregonensis*, *Epischura lacustris*, *Eurytemora affinis*, *Daphnia galeata mendotae*, *Diaphanasoma* spp., and *Eubosmina coregoni* exhibited a stronger decline in abundance over 1982–84. In addition, nauplii abundances during 1982–84 were only 3% of the 1975–81 average. Although nauplii are small, their abundances ultimately are determined by the abundances of the larger adult copepods. *Chydorus sphaericus* and *Polyphemus pediculus* were the only taxa to occur in similar abundances over the two time periods (Table 1).

Discussion

Alewife standing stocks have declined markedly in Lake Michigan, with the beginning of the decline first becoming evident in 1978 (Jude and Tesar 1985; Evans and Jude 1986). In the Donald C. Cook study area, fish were collected between the 5- and 10-m depth contours using gill nets and trawls. Average summer (July–August mean) catch-per-unit-effort of age 1 and older alewife decreased from 1199 (±781) for 1973–77 to 408 (±110) for 1978–81. In summer 1982, the mean catch-per-unit-effort of age 1 and older alewife was only 115 (Evans and Jude 1986). Young-of-the-year catches also declined over 1973–77 (277 ± 516) to 1978–81 (20 ± 28). Although a larger number (971) of young-of-the-year were collected in gill nets and trawls in summer 1982, catches were lower in the beach seine collections. This suggests that young-of-the-year were not more abundant in summer 1982 but had simply moved farther offshore (Evans and Jude 1986). Recent studies suggest that alewife may have been displaced from their preferred thermal regime by other forage fish species which increased in abundance as alewife abundances declined (Crowder and Magnuson 1982).

Comparable fisheries data were not collected in the Cook study area after 1982. However, data collected by other researchers document the continued lake-wide decline in alewife abundances. Wells and Hatch (1984) reported that the 1983 autumn catch of age 1 and older alewife was only about 33% of the 1982 catch and 17% of the 1981 catch. Similarly low catches were observed in 1984 (L. Wells, pers. comm.).

In the offshore region of southeastern Lake Michigan, reductions in alewife standing stocks over 1978–84 cooccurred with pronounced changes in the summer zooplankton community.

TABLE 1. Mean summer (July–August average) abundance and percent composition of zooplankton in the inshore region (5- to 10-m depth contours) over 1975–81. Also shown is the mean abundance of zooplankton in the intake waters of the D. C. Cook Nuclear Plant over 1975–81 and 1982–84. See text for further explanation.

	Mean abundance (no./m^3)			Mean composition (%)		
	Inshore, 1975–81	Intake		Inshore, 1975–81	Intake	
		1975–81	1982–84		1975–81	1982–84
Copepods						
Nauplii	3 771	3 050	93	8.3	5.1	1.6
Cyclops spp. C1–C5	3 102	7 375	868	6.8	12.2	14.7
C. bicuspidatus thomasi C6	249	816	18	0.6	1.4	0.3
Tropocyclops sp. C1–C5	106	79	20	0.2	0.1	0.3
T. prasinus mexicanus C6	433	378	34	1.0	0.6	0.6
Diaptomus spp. C1–C5	2 293	3 418	245	5.0	5.7	4.2
D. ashlandi C6	109	244	7	0.3	0.4	0.1
D. minutus C6	526	326	22	1.2	0.5	0.4
D. oregonensis C6	18	42	2	0.0	0.1	0.0
D. sicilis C6	15	13	4	0.0	0.0	0.1
Epischura sp. C1–C5	193	208	4	0.4	0.4	0.1
E. lacustris C6	6	18	3	0.0	0.0	0.1
Eurytemora sp. C1–C5	811	843	44	1.8	1.4	0.8
E. affinis C6	27	162	9	0.1	0.3	0.2
Cladocerans						
Bosmina longirostris	30 321	39 177	3451	66.5	65.0	58.5
Ceriodaphnia lacustris	136	88	0	0.3	0.2	—
Chydorus sphaericus	90	219	517	0.2	0.4	8.8
Daphnia galeata mendotae	93	89	0	0.2	0.2	—
D. retrocurva	876	1 705	215	1.9	2.8	3.6
Diaphanosoma spp.	230	108	0	0.5	0.2	—
Eubosmina coregoni	277	204	2	0.6	0.3	0.0
Holopedium gibberum	67	64	4	0.2	0.1	0.1
Leptodora kindtii	33	27	0	0.1	0.0	—
Polyphemus pediculus	101	49	34	0.2	0.1	0.6
Rotifers						
Asplanchna spp.	1 430	737	45	3.1	1.2	0.8
Rare taxa	293	832	259	0.6	1.4	4.4
Total	45 606	60 271	5900			

Large species of *Daphnia* increased in dominance. Furthermore, *Daphnia pulicaria*, a very large species, became a new dominant of the summer 1982–84 plankton (Evans 1985; Evans and Jude 1986). However, the inshore region *Daphnia* did not show a similar response. The smallest species, *Daphnia retrocurva* (mean dry weight 2.0 μg; Hawkins and Evans 1979), continued to dominate the *Daphnia* assemblage. In addition, abundances of this small species were strongly reduced over the summer periods of 1981–84 (Evans and Jude 1986). This suggests that predation pressure on the *Daphnia* community remained high between 1978 and 1980 and intensified over summer 1981–84.

Inshore, total crustacean zooplankton structure remained unchanged over summer 1981–84, with small taxa continuing to predominate (Table 1). However, standing stocks were reduced, with abundances over 1982–84 only 10% of the intake mean for 1975–81. This strong reduction in zooplankton abundances and the continued trend for the community to be dominated by small taxa suggest that predation pressures exerted by planktivorous fish not only remained high as alewife abundances declined but also intensified over 1982–84. Furthermore, such predation pressures must have been exerted by fish which were abundant inshore but not offshore. This corollary is necessary because larger *Daphnia* did increase in abundance offshore as alewife numbers declined.

Yellow perch is the second most abundant planktivorous fish inshore. Unlike alewife, which occur across the lake, yellow perch are located primarily inshore during warm summer months (Wells 1968). Yellow perch spawn in late spring with young-of-the-year appearing in June. In their first 2 yr of life, yellow perch are concentrated in waters shallower than 6 m (Wells 1968).

Average summer catch-per-unit-effort (gill nets and trawls) of age 1 and older adult yellow perch remained more or less constant in the inshore region between summer 1973 and 1980 (mean = 514 ± 211) (Evans and Jude 1986). However, as alewife abundances declined through the early 1980s, yellow perch abundances increased (Jude and Tesar 1985; Evans and Jude 1986). Average summer catch-per-unit-effort of juveniles and adults increased to 2051 in 1981 and averaged 1358 in summer 1982. Young-of-the-year yellow perch were especially abundant in summer 1982, with the catch averaging 593 fish versus 29 (±25) for 1973–77 and 74 (±92) for 1978–81 (Evans and Jude 1986). Comparable data were not collected in the Cook study region after summer 1982. However, Wells and Hatch (1984) reported that yellow perch catches were 50 times larger in autumn 1983 than any catch over the previous 20 yr of sampling. Yellow perch were similarly abundant in autumn 1984 (L. Wells, pers. comm.).

Larval and young-of-the-year yellow perch are planktivorous, while older juveniles and adults feed most intensively on larger, benthic organisms (Scott and Crossman 1973; Keast 1977). Previous studies have shown that yellow perch can affect *Daphnia* community structure, eliminating larger taxa from the plankton (Galbraith 1967; Mills and Forney 1983). My results suggest that as young-of-the-year yellow perch increased in abundance in summer 1982, 1983, and 1984, predation pressure on the zooplankton community intensified. Such predation pressures must have been especially great within the 5-m contour, the region of highest summer concentrations of yellow perch (Wells 1968). As a probable consequence of intense yellow perch predation, zooplankton standing stocks were reduced severalfold.

Intense planktivory has the potential to adversely affect predators if food resources become limiting. Young-of-the-year yellow perch apparently consumed large numbers of zooplankton during 1982−84, depleting zooplankton resources. This resource limitation must have been especially severe in summer 1984 when zooplankton standing stocks (numerical, biomass) reached only 3% of their average abundance over 1975−81. At this time, food resources may not have been sufficiently high to meet metabolic needs of the large numbers of planktivorous young-of-the-year yellow perch present in the inshore region. Furthermore, the growth of juveniles may have been adversely affected. L. Wells (pers. comm.) reported that the 1983 population of yellow perch has grown extremely slowly. Fish at the end of 2 yr reached a body length of only 100 mm in comparison to a typical body length of 160 mm in the 1970s. Preliminary studies suggest that the 1984 class of young-of-the-year are similarly stunted (L. Wells, pers. comm.).

Other changes occurred in the Lake Michigan forage fish community as alewife numbers declined. Bloaters (*Coregonus hoyi*) increased in abundance in the late 1970s and early 1980s (Well and Hatch 1984; Jude and Tesar 1985; L. Wells, pers. comm.). However, bloaters were not a major component of the summer inshore fish community (Evans and Jude 1986). Thus, they are unlikely to have had as major an effect on zooplankton populations as yellow perch.

Although blue-green algae increased in abundance (but not necessarily in biomass) in the inshore region over the course of the phytoplankton monitoring studies (Ayers and Feldt 1982, 1983), it is unlikely that a continuation of such changes resulted in a major reduction in zooplankton standing stocks over summer 1982−84. If eutrophication were an important factor affecting the summer zooplankton population at this time, zooplankton community structure should have shifted toward a greater dominance of species indicative of nutrient-enriched waters, e.g. *Bosmina longirostris*, *Chydorus sphaericus*, *Cyclops* spp., and *Eurytemora affinis*. Such changes were not observed. Furthermore, while *Chydorus sphaericus* increased in abundance over 1982−84, this increase probably was related to the small size of this species and the reduced abundance of larger competing species. *Polyphemus pediculus*, another small cladoceran, also increased in abundance over the summer 1982−84 period. In the summer of 1966, Wells (1970) noted an increase in small zooplankton abundances (including *Polyphemus pediculus*) as alewife severely reduced abundances of the larger zooplankton.

Zooplankton standing stocks were especially low (1938/m^3) in summer of 1984, reaching only 3% of the average value for 1975−81. Such a reduction in total zooplankton standing stocks has not been previously observed in lakes into which planktivores have been introduced. While mysid introduction apparently resulted in the elimination of several zooplankton species in the open waters of Lake Tahoe, this system is ultraoligotrophic (Goldman et al. 1979). Thus, zooplankton populations may not have had sufficient resilence (because of severe food limitations) to withstand a substantial increase in predation-induced mortality. In contrast, Lake Michigan is more productive, bordering between oligotrophy and mesotrophy (Chapra and Robertson 1977). Furthermore, some exchange of inshore and offshore water occurs during all seasons. As stated earlier, zooplankton standing stocks were not reduced in the offshore region over 1982−84 and, in fact, shifted in composition toward a greater dominance of large *Daphnia* spp. (Evans and Jude 1986). Given the probable exchange of inshore and offshore water, the strong reduction of zooplankton standing stocks in the narrow band of inshore water over 1982−84 is all the more striking.

Although zooplankton standing stocks were severely depressed over summer 1982−84, it is unlikely that such reductions will continue much further into the future. Increased food limitation apparently resulted in the stunted growth of the 1983 and 1984 yellow perch year classes. This suggests that yellow perch began to exceed the carrying capacity of the inshore region over 1983−84. Consequently, feedback mechanisms such as reduced fecundity and cannibalism on earlier life history stages may intensify, resulting in a reduction in yellow perch populations to levels more typical to those observed during the 1970s. There is some evidence that such feedback mechanisms have begun to operate. In summer 1985, zooplankton abundances increased in intake waters, averaging 47 765/m^3 (22 155 /m^3 in July and 73 376/m^3 in August), in comparison with 7318/m^3 over 1982−84. Furthermore, while the small-bodied *Bosmina longirostris* was the major component (68.3%) of the zooplankton community, the larger *Daphnia retrocurva* accounted for 13.3% of the average numerical standing stock. Other dominant taxa included immature *Cyclops* spp. copepodites (5.7%), immature *Diaptomus* spp. copepodites (4.4%), *Asplanchna* spp. (3.4%), and immature *Epischura* spp. copepodites (2.4%). The increased abundance of total zooplankton and the increased dominance of larger-bodied taxa such as *Daphnia retrocurva* suggests that planktivory was less intense in summer 1985 than summer 1982−84. Thus, I hypothesize that predation pressures exerted on the inshore region zooplankton community by planktivorous fish began to relax in summer 1985, approaching levels more typical to those observed in the 1970s. Such a reduction in predation pressure does not appear to be directly associated with yearling and older yellow perch. Preliminary studies, based on trawl collections made in the inshore region in summer 1985, suggest that the 1983 and 1984 year classes of yellow perch remain abundant, while alewife abundances remain low (G. Noguchi and T. Wells, U.S. Fish and Wildlife Service, Ann Arbor, MI, pers. comm.). Therefore, apparent reductions in fish predation pressures on the summer inshore zooplankton community must have been associated with larval and young-of-the-year yellow perch. Thus, I hypothesize that, because of the intensification of feedback mechanisms (possibly cannibalism), larvae and young-of-the-year yellow perch were less abundant in summer 1985 than during summer 1982−84.

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Individual Parameter Perturbation and Error Analysis of Fish Bioenergetics Models[1]

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We quantified the sensitivity of predicted rates of growth and consumption to parameter variation for models of yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), and alewife (*Alosa pseudoharengus*). We used statistical analyses of the results of Monte Carlo simulations to rank parameter importance. The order of parameter importance was model specific, although the results emphasized the need for accurate estimation of the realized fraction of maximum consumption rate (P) and allometric parameters for consumption (a_1, b_1) and respiration (a_2, b_2). Excretion and egestion parameters contributed little to prediction errors. The Monte Carlo methods were used to examine the relative importance of parameter variation and diet composition, an external forcing function, on forecasts of alewife growth. If standard deviations of model parameters were known within 2% of their expected values, uncertainty in diet composition could contribute as much as 47% of the variance in predicted alewife weight. When standard deviations of model parameters are realistically defined, diet uncertainty contributed less than 10% of the variance in predicted weight.

Nous avons évalué la précision des taux prévus de croissance et de consommation quand les paramètres varient pour des modèles de perchaude (*Perca flavescens*), d'achigan à grande bouche (*Micropterus salmoides*) et de gaspareau (*Alosa pseudoharengus*). Nous avons fait des analyses statistiques des résultats obtenus à partir de simulations Monte-Carlo pour évaluer l'importance des paramètres. L'ordre d'importance des paramètres variait selon le modèle, bien que les résultats aient fait ressortir la nécessité d'évaluer de façon précise la partie atteinte du taux maximum de consommation (P) et les paramètres allométriques de consommation (a_1, b_1) et de respiration (a_2, b_2). Les paramètres d'excrétion de d'évacuation ont peu contribué aux erreurs de prévision. On s'est servi des méthodes Monte-Carlo pour évaluer l'importance relative de la variation des paramètres et de la composition du régime alimentaire, qui est un facteur externe déterminant, sur les prévisions de croissance des gaspareaux. Si l'on connaissait la déviation standard des paramètres du modèle à 2 % près des valeurs prévues, l'incertitude liée à la composition du régime alimentaire pourrait expliquer jusqu'à 47 % de la variance du poids prévu des gaspareaux. Lorsque la déviation standard des paramètres du modèle est définie de façon réaliste, l'incertitude liée au régime alimentaire explique moins de 10 % de la variance du poids prévu.

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Mathematical models that describe growth as an integration of rate-specific physiological processes have been used to study the production dynamics of fishes (Kitchell and Breck 1980; Kitchell et al. 1974, 1977; Rice and Cochran 1984; Rice et al. 1983; Stewart et al. 1981, 1983). The usefulness of these models for developing and testing hypotheses concerning the dynamics of fish growth depends in part on the availability and quality of information necessary to derive model parameters. Specific model applications commonly require the collation of several data sets from different fish species in order to estimate parameter values (e.g. Kitchell et al. 1974; Kitchell and Breck 1980; Rice et al. 1983). Error introduced by amalgamation of parameters derived from different taxa and complicated by error in experimental measurements within taxa could bias simulated growth.

Sensitivity analyses have been performed for several of the models to examine the implications of parameter uncertainty on fish growth (i.e. Kitchell et al. 1977; Rice et al. 1983; Stewart et al. 1981, 1983). These analyses used individual parameter perturbations (IPP) to approximate the partial derivatives of model equations with respect to each parameter (Byrlinsky 1972). Single parameter values were increased or decreased by a constant fraction, while remaining parameters were fixed at their nominal values. Relative changes in selected model predictions, for example, yearly fish growth (Kitchell et al. 1977) or consumption rate (Rice et al. 1983), were used to assess sensitivities.

The IPP approximation to sensitivity analysis has the potential to bias results (Gardner et al. 1981). If model processes are represented by nonlinear functions, the IPP method can generate poor estimates of true partial derivatives. Rank orders of parameter sensitivities thus estimated could be incorrect. Sensitivity analysis also implies that the expected behavior of the

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TABLE 1. Equations for bioenergetic models of perch (Kitchell et al. 1977), largemouth bass (Rice et al. 1983), and alewife (Stewart 1980). Notation was retained from the original presentation whenever possible.

Perch

$$\frac{dB}{Bdt} = a_1 B^{b_1} \cdot P \cdot r_C (1 - s - \alpha_1 T^{\beta_1} \cdot e^{\gamma_1 P} - \alpha_2 T^{\beta_2} \cdot e^{\gamma_2 P}) - a_2 B^{b_2} \cdot A \cdot r_R$$

Largemouth bass

$$\frac{dB}{Bdt} = a_1 B^{b_1} \cdot P \cdot r_C (1 - s - f - u) - a_2 B^{b_2} \cdot e^{mT} \cdot e^{gS}$$

Alewife

$$\frac{dB}{Bdt} = a_1 B^{b_1} \cdot P \cdot r_C (1 - s - \alpha_1 T^{\beta_1} \cdot e^{\gamma_1 P} - \alpha_2 T^{\beta_2} \cdot e^{\gamma_2 P}) - a_2 B^{b_2} \cdot e^{mT} \cdot e^{gS(T.w)}$$

model is equal to that observed with all parameters set at their mean (estimated) values. The higher order effects that can result from parameter covariances are ignored. To minimize numerical pitfalls, numerical sensitivity analysis necessarily focuses on the effects of small perturbations of single parameters; the effects of larger errors cannot be reliably considered.

Error analysis represents an alternative evaluation of the contribution of parameter variation to prediction error. This method directly addresses the numerical problems of IPP and obviates the assumptions implied in sensitivity analysis. In error analysis, the nominal values of model parameters are treated as the expected values of statistical distributions defined for each parameter. Sets of parameter values are sampled independently from their distributions in repeated model realizations. These Monte Carlo simulations produce sets of model predictions where the variance is a function of parameter variability as translated by the model equations. The variance can be exploited by statistical analysis to quantify the dependence of model predictions on parameter uncertainty (Bartell et al. 1983; Gardner et al. 1980a, 1980b, 1980c, 1981; O'Neill et al. 1980, 1981). Error analysis, as we have defined it, focuses on model precision given uncertain parameter values. Other sources of error, especially as they may affect model accuracy, have been examined by Gardner et al. (1981) for a variety of ecological models.

Model imprecision is not only a function of parameter variation but is also affected by uncertainties associated with values of external inputs that drive the model. The methods of error analysis permit the expected variation (empirical or theoretical) to be expressed as distributions assigned to model inputs. Repeated simulations with independently chosen values can be used to quantify the dependence of model predictions over a continuous range of expected input variability. Performed in combination with variation of internal parameter values, error analysis can quantify the relative impact of variation in external inputs versus internal parameters on model predictions.

Research reported in this paper compares results of previous IPP studies (Kitchell et al. 1977; Rice et al. 1983) with results of error analysis for three species-specific (yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), and alewife (*Alosa pseudoharengus*)) versions of the bioenergetics models. We also examined the speculation that these models are more precise in estimating fish feeding rates (given observed patterns of growth) than in forecasting fish growth (given estimates of parameters that determine feeding rates) (Kitchell et al. 1977). Lastly, we characterized the relative importance of variation in internal model parameters versus variation in an external variable, diet composition, in predicting alewife growth.

Model Description

The bioenergetics models of fish biomass (B) included in these analyses derive from the same underlying equation. Specific growth rate (dB/Bdt) is a function of rates of consumption (C), respiration (R), egestion (F), and excretion (U):

(1) $dB/Bdt = C - (R + F + U)$.

Different formulations of these growth processes distinguish the separate models of yellow perch, largemouth bass, and alewife (Table 1). Biological differences in growth processes and the availability of data for parameter estimation produced the species-specific formulations. Rates of consumption and respiration are nonlinear functions of fish weight and water temperature. The value of P determines the fraction of the weight-dependent maximum consumption rate realized during each daily time step. The particular temperature-dependent functions that affect rates of consumption (r_C) and respiration (r_R) are detailed elsewhere for these species (Kitchell et al. 1977; Rice et al. 1983; Thornton and Lessem 1978). Though slightly different, these functions require specification of a temperature where the maximum rate is observed (T_0), an upper limiting temperature (T_m), and a parameter (Q) that determines the slope of the function between 0°C and T_0.

The models differ in their expressions for rates of egestion, excretion, and their representations of respiration in relation to specific dynamic action and swimming activity. For example, egestion and excretion are nonlinear functions of temperature and feeding in the perch and alewife models (Table 1), based on the extensive study of brown trout (*Salmo trutta*) by Elliott (1976). This contrasts with the linear rates suggested by the investigations of Beamish (1974) and Niimi and Beamish (1974) and used in the bass model (Rice et al. 1983).

The models also differ in their representation of prey availability. For example, specific prey items are not identified in the perch or bass models and prey energetic quality is considered constant. Prey preference varies seasonally in the alewife model and differs for subsequent age classes of alewife (Stewart 1980).

The original models have been applied in two ways. First, using estimates of maximum consumption rates and fixed P values, the models have been used to estimate fish growth through time (Kitchell et al. 1974). Second, the models have been used to estimate seasonal patterns of consumption by varying P to fit the model to observed patterns of fish growth (e.g. Kitchell et al. 1977; Rice et al. 1983). We used published values of parameters for the models of perch (Kitchell et al. 1977), largemouth bass (Rice et al. 1983), and two age-classes of alewife (Stewart 1980) in our analyses. We retained the original notation whenever possible.

Methods of Analysis

The error analysis of each fish model (Table 1) proceeded as follows. Statistical distributions were assigned to all parameters included in previous sensitivity (IPP) analyses by using the nominal values as the mean values of normal distributions. A deterministic simulation that used the parameter values reported for the IPP analyses was performed for each of the species-specific models. Results of these simulations were compared with results reported previously as a check for correct model implementation. In each error analysis, 150 simulations were performed for each model with parameter values chosen from their distributions by means of a stratified random sampling method (Iman and Conover 1980). The analyses were performed with three levels of parameter variation. These levels are conveniently described by coefficients of variation (CVs) equal to 2, 10, and 20%. These CVs were chosen because (1) Gardner et al. (1981) suggested that error analysis with 2% CVs on all parameters provides an adequate approximation to the partial derivatives in analytical sensitivity analysis, (2) the previous IPP analyses used parameter variations that were 10% increases or decreases from the nominal values, and (3) O'Neill et al. (1980) surmised that ecological parameters might be routinely measured with standard deviations no smaller than 20% of their mean values. Following each simulation, temporal values of fish weight or rates of consumption were recorded with their corresponding parameter values for statistical evaluation of parameter importance.

For each method, criteria were chosen by which the relative importance of model parameters was assessed. In the IPP analyses, parameter importance was evaluated by calculating the percent change in normalized growth rate or consumption rate that resulted when individual parameters were changed by ±10%. In the error analyses, parameters were ranked in importance by quantifying their contribution to explaining variance in the model predictions produced by Monte Carlo simulation. Relative partial correlation coefficients can be used to rank parameters (Gardner et al. 1981); however, parameters can show high correlation yet account for small residual variances. The relative partial sum of squares (RPSS) quantifies the amount of residual variance accounted for by individual parameter variation after the effects of all other parameters have been statistically removed. The RPSS, therefore, provides a better estimate of the sensitivity of the prediction variable to individual parameter variation. We used the RPSS to rank parameters in our analyses for comparison with ranks derived from the previously reported IPP analyses. The RPSS indicate the expected increase in model precision when all parameters can be more precisely estimated. Simple correlation (e.g. Spearman) can also be used to rank parameter importance. Simple correlations indicate the fraction of total variance in the prediction variable explained by variation in single parameters; the effects of the remaining parameters are not removed. Simple correlations also quantify the expected increase in model precision that would result from improved estimation of an individual parameter when all other parameter values remained unchanged.

TABLE 2. Rank order of top 10 parameters (including ties) that results from individual parameter perturbation of the perch model (Kitchell et al. 1977) and error analyses with coefficients of variation of parameter values set at 2, 10, and 20%. Nominal parameter values are in parentheses.

Parameter	Individual parameter perturbation	Error analysis (CVs) 2%	10%	20%
Consumption				
P (0.378)	1	2	2	2
a_1 (0.250)	1	1	1	1
b_1 (−0.270)	3	4	3	3
T_0 (23)	6	3	6	
T_m (28)				
Q_c (2.300)	8	8	8	6
Respiration				
SDA (0.15)				8
a_2 (0.035)	3	6	4	4
b_2 (−0.200)		9	9	10
T_0 (28)	9	5	5	
T_m (33)				
Q_R (2.1)	6	7	7	5
A (1.0)	3			7
Egestion, excretion				
α_1 (0.158)				
β_1 (−0.222)	8			
γ_1 (0.631)				
α_2 (0.0292)				
β_2 (0.58)		10	10	9
γ_2 (−0.299)				
R^2		0.99	0.97	0.93

The statistical analyses of the results of the Monte Carlo simulations relied on the use of linear models that summarized variance in the predictions in direct relation to parameter variation. Thus, the R^2 statistic indicated the relative importance of direct parameter effects on fish growth or consumption rate. The residual variance ($1 - R^2$) was proportional to model behavior that resulted from interaction effects among parameters and nonlinear relationships between model results and parameter values.

Results

Perch Model

Error analysis was used to examine parameter contribution to error in predicting yearly growth of an age I+ yellow perch with an initial weight of 9 g under conditions described in Kitchell et al. (1977). Table 2 lists the top 10 (including ties) ranked parameters from the IPP analysis (Kitchell et al. 1977, fig. 6) with the ranks from the error analyses.

Despite the potential problems of the IPP analysis, the results of Kitchell et al. (1977) are very similar to the rankings that resulted from error analysis with CVs of 2%. Parameters P and a_1 consistently ranked highest in their contribution to variability in the final weight of yellow perch. Parameters b_1 and a_2 also ranked high in the analysis. From examination of the equation for perch growth (Table 1), we suggest why these parameters

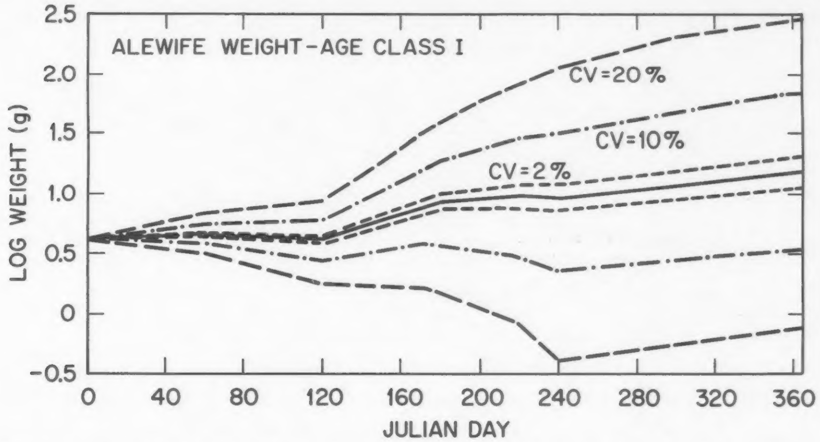

FIG. 1. Logarithm$_{10}$ of simulated wet weight of age-class I alewife vs. time. Solid line is the deterministic solution. Lines above and below designate the 5th and 95th percentile values from 150 simulations at each of three levels of parameter variation: coefficients of variation equal 2, 10, and 20%, respectively.

TABLE 3. Comparison of parameter importance for largemouth bass model used to predict consumption. Ranks from Rice et al. (1983) estimated from individual parameter perturbation. Error analysis used 10% CVs for parameters. Relative partial sums of squares (RPSS) were used to rank parameters in error analysis. Nominal parameter values are in parentheses.

	Parameter rank order		
Parameter	Rice et al. 1983	Error analysis	RPSS
S (0.142)	4	2	0.309
f (0.104)	5	3	0.147
u (0.079)	6	4	0.090
a_2 (0.0271)	2	5	0.039
b_2 (−0.355)	1	1	0.323
m (0.0313)	3	6	0.030
g (0.0196)	7	7	0.028
R^2			0.966

can assume importance. Parameter P is an exponent in the egestion and excretion terms and a multiplier of consumption, egestion, and excretion rates. The mean value of P (0.522) is also of similar magnitude to γ_1 and nearly twice as large as the absolute value of γ_2 (0.299). Therefore, P is in the mathematical position to heavily influence the overall growth rate. The a_1 parameter similarly multiplies the consumption, egestion, and excretion terms. In addition, a_1 is part of the term for specific dynamic action, which subtracts linearly from the consumption rate in the perch model. The values of the R^2 statistic (Table 2) indicate that linear relations between parameter values and model predictions accounted for more than 90% of the variability in final perch weight in these analyses.

The IPP and error analyses differed in their ranking of the activity parameter A. When parameters were varied one at a time by 10%, b_1, a_2, and A contributed similarly at rank 3 to prediction error. When all parameters were varied simultaneously, b_1 retained its importance, but a_2 and A diminished in rank. The results further demonstrated that the rank order of parameter importance was influenced by the magnitude of parameter uncertainty. While P and a_1 retained their rank as their variability increased, several parameters (b_1, Q_c, S, a_2, Q_R, A, and β_2) increased in importance. By comparison, T_0 for consumption, b_2, and T_0 for respiration contributed less to variance in simulated perch weight as parameter variation increased. The changing patterns of parameter importance demonstrated that results of IPP analysis must be interpreted with caution, especially if data indicate parameter variations in excess of 10% of their expected values.

Results of the IPP analysis (Kitchell et al. 1977) and the error analyses indicated that the perch model could be simplified to a temperature-dependent feeding model without major loss of ability to predict perch growth. The parameter rankings (Table 2) can order future research priorities to refine critical model parameters. Experiments that measure rates of consumption and respiration in relation to fish weight and water temperature will contribute to increased precision in predicted perch growth.

Largemouth Bass Model

Error analyses were performed on the largemouth bass model (Rice et al. 1983) to compare resulting parameter importances with those identified by IPP analysis. Here, emphasis was placed on the sensitivity of growth rate (dB/dt) to variation in model parameters that did not directly determine rates of consumption (Table 3). The pattern of parameter ranks generated by the error analysis was the same for the three levels of parameter variation. Only the results from the 10% CV case are presented along with the pattern of ranks reported by Rice et al. (1983). In comparison with the IPP results, the order of parameter importance was the same for the most important, b_2, and least important, g, parameters. However, the error analysis identified S, the specific dynamic action coefficient, as the second most important contributor to variation in growth rate, while the IPP analysis ranked a_2 second. The analyses also differed substantially in the ranking of m. The order of S, f, and u, was maintained in both analyses, but these parameters ranked consistently higher in their contribution to prediction variability in the error analysis than in the IPP analysis. The partial sums of squares (Table 3) indicate that only three param-

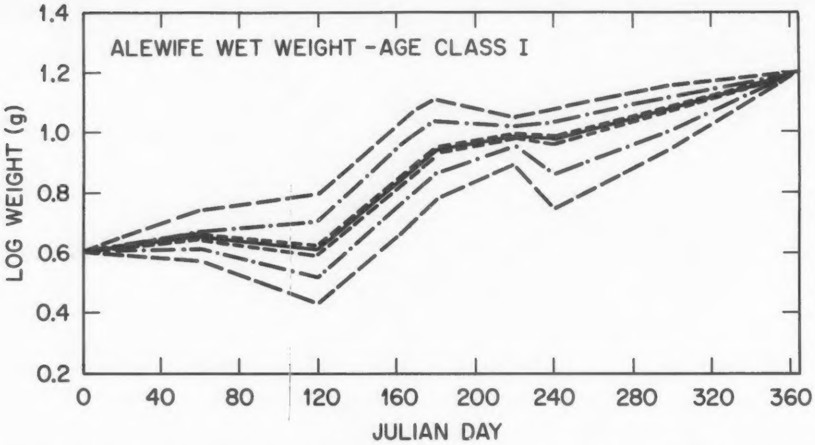

FIG. 2. Logarithm$_{10}$ of simulated wet weight of age-class I alewife constrained to fit final weight of 16 g. Solid line shows the deterministic solution. Lines above and below designate the 5th and 95th percentile values from 150 simulations at each of three levels of parameter variation: coefficients of parameter variation are 2, 10, and 20%, respectively.

eters carry appreciable weight in the analysis, b_2, S, and f. Similar to the analysis of the perch model, the R^2 value of 0.96 hinted that interactions among parameters and nonlinear effects were unimportant in the error analyses of the bass model.

Alewife Model

Kitchell et al. (1977) and Stewart et al. (1983) concluded that the bioenergetics models were more precise in applications where consumption rates were calculated to fit observed fish growth than when estimates of consumption rates and initial conditions were extrapolated to predict fish growth. We examined this premise for the alewife model (Stewart 1980). Figure 1 illustrates the effects of parameter variation on weight of an age-class I alewife during a single year of growth. From an initial wet weight of 4 g, the deterministic simulation grew the fish to 16 g by the end of 1 year. Figure 1 shows the 5th and 95th percentiles from 150 simulations for each of three levels of parameter variation. For each degree of parameter imprecision, the pattern of growth deviated increasingly through time from the deterministic solution. This pattern was partially the result of seasonal changes in water temperature, which increased rates of consumption. Similar to results for the perch and bass models, the increase in variation of predicted alewife wet weight originated from amplification of variability of the parameters that determined feeding rate. When the standard deviations of the parameters were 20% of their mean values, 5% of the fish exceeded 240 g after 1 yr of growth. Similarly, 5% of the fish weighed less than 0.6 g. For CVs of 10%, extreme values exceeded 55 g or were less than 2.7 g. Symmetry about the deterministic simulation demonstrated that model imprecision approximated a log-linear function of imprecision in estimates of the parameters. The symmetry deteriorated between days 120 and 240 when parameter variability in the 10 and 20% CV cases produced highly negative energy budgets in some simulations.

Figure 2 presents the temporal weight for the age-class I alewife when the parameter P was adjusted to constrain consumption rates to grow a 4-g fish to the observed weight of 16 g. The results confirmed the model behavior suspected by Kitchell et al. (1977). For all three degrees of parameter variation, model behavior varied less than when the model was used to estimate final weight from initial conditions. These results also emphasize the leverage that P has on the overall behavior of the model, as suggested from the mathematical formulations in Table 1. When the model was constrained to fit observed endpoints of growth, parameter variability only contributed to variance in the pattern of growth predicted between observations. At each time corresponding to a growth measurement, the model was forced to exhibit zero bias. This limited the accumulation of prediction error to the time intervals between the observed growth. Differences in patterns of error propagation in the two modes of application of the alewife model produced different rank orders of parameter importance (Fig. 3). When the model was used to forecast yearly growth, a pattern of parameter importance similar to that found for the perch model obtained. Parameters a_1 and P ranked first and second; the RPSS values show their similarity in importance. Likewise, a_2 and b_1 ranked high, as in the perch model. Consistent with previous analyses, the egestion and excretion parameters contributed minimally to imprecision in predicted wet weight.

It may be reasonable to presume that when the model is used to fit growth that the rank 2 parameter P, now removed from the analysis, will simply be replaced by the third ranked parameter and that other parameters will follow in order. Figure 3 shows that this was not the case. The previously important parameters ranked no higher than eighth. Variation in wet weight between points of observed growth became subsequently determined by variability in parameters that defined the relationships between water temperature and rates of consumption (r_C) and respiration (r_R). Adjustments of P constrained the influence of a_1 and b_1.

The differences in parameter importance for the two uses of the model might be used to organize efforts aimed at increasing model precision. To forecast growth from initial conditions more precisely, experimental resources should be directed at refining the allometric relationships for consumption and respiration. Accurate estimates of the realized fraction of maximum consumption, P, must be obtained by whatever means pos-

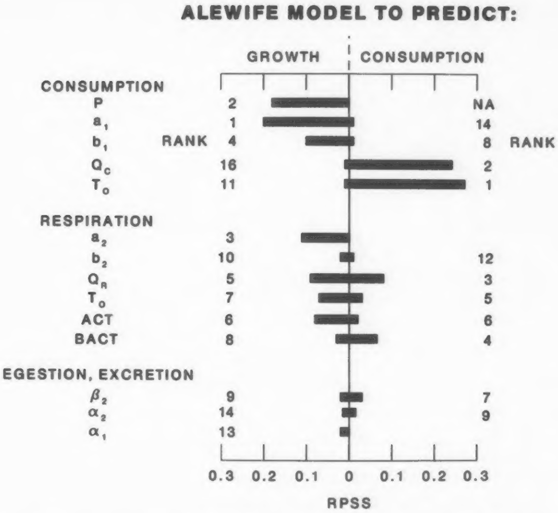

FIG. 3. Ranks and relative partial sums of squares (RPSS) for parameters of the alewife model used to forecast growth or estimate consumption.

sible. Alternatively, if the model is to be used to estimate consumption rates consistent with observed growth, experiments should focus on the temperature dependence of consumption and respiration, as well as accurate accounting of the thermal history of the fish.

Changes in the rates of deviation from the deterministic solution in Fig. 1 suggested that the relative importance of parameters may have varied during the course of a simulation. To address this, we calculated the RPSS for parameters previously identified as important at selected times during the course of simulation of the growth of age-class I alewife. The 20% CV case for the parameters was chosen for presentation, although similar patterns result from the 2 and 10% cases. Results show that the rank order of parameter contribution to variance in alewife wet weight was time dependent (Fig. 4). On day 365, the familiar pattern occurred: P and a_1 were the most important parameters. However, for the first 150 d of growth, the respiration parameter a_2 explained most of the variability in fish growth. The slope of the temperature-dependent function for consumption, Q_C, ranked second between days 40 and 130. These changes in rank order were the direct consequence of the model structure and daily input values of water temperature. Low temperatures limited feeding rates during the initial segment of the growing season. A slight increase in the Q_{10}-like temperature dependence at this time of year will increase consumption rates nonlinearly. During periods of forced low consumption rates, respiration dominated growth, and a_2, which defines the maximum respiration rate, became the most important parameter.

The results illustrated in Fig. 4 emphasize an important point concerning sensitivity analyses. Namely, the sensitivities depend on the question asked of the model. Global assertions about the relative importance of model parameters are to be made cautiously. Parameter rankings may depend on the shape of the seasonal temperature function, for example, and parameter importance might change in specific model applications. The time-varying change in the rank order of parameter importance noted in other models of similar structure (e.g. Bartell et al. 1983) is further reason for restraint in drawing conclusions about the general importance of model parameters from limited analysis.

Simple Correlation and Parameter Importance

The previous error analyses of the fish models identified the rank order of importance of parameter values and demonstrated that such order was a function of model use. The rank order was also shown to be time dependent. Rank was assigned in direct proportion to the residual variance explained by individual parameters when the variance explained by all other parameters was removed. Alternatively, simple correlation can be used to relate variation in prediction variables to parameter uncertainty. Parameters that appear unrelated from inspection of model structure can show covariance, especially if the values are systematically modified during a simulation. For example, daily values of water temperature adjust rates of both consumption and respiration in the fish models (Kitchell et al. 1974). Although maximum feeding and respiration rates might be calculated independently for a species, the realized fractions of these maxima can increase or decrease together on a daily basis as water temperature changes. Such parameter covariances might increase, decrease, or compensate in their effects on variability in model predictions.

To identify similarities in parameter behavior, Spearman correlation coefficients were calculated between individual parameter values and predicted wet weights for age-class I alewife. The coefficients ranged between 0.6 and −0.6. The results highlighted the positive correlation between feeding parameters and wet weight and the negative correlation between respiration parameters and wet weight. Parameters a_1, P, b_1, and a_2 combined to account for approximately 70% of the variance in predicted wet weight. The simple correlations did not exhibit the same degree of temporal changes in order of importance as in the RPSS calculations (Fig. 4). Parameters remained either positively or negatively correlated with variance in predicted wet weights throughout the course of the simulations. The simple correlations also quantified the expected improvement in model precision given refinement in estimates of individual parameters when remaining parameters cannot be improved. A 10% increase in precision in estimating P, for example, will produce an approximate 10% decrease in variance of predicted wet weight, even if other parameters cannot be better estimated.

Uncertainty in Diet Composition vs. Parameter Variation

Our analyses have detailed the effects of parameter variability on model behavior for different formulations of the fish model. For each model, additional uncertainty can be introduced by variability associated with required input data. Sources of variability include bias and imprecision in measurement and environmental heterogeneity. The relative sensitivity of model predictions to parameter uncertainties versus uncertainties in external inputs can be quantified with the methods of error analysis.

We examined the relative importance of parameter versus input variability for the alewife model. Rice and Cochran (1984) previously characterized the sensitivity of simulated bass growth to systematic variation in water temperature. In addition to water temperature, the alewife model required daily values of diet composition formulated as the fraction of total diet apportioned among each of four prey categories: *Pon-*

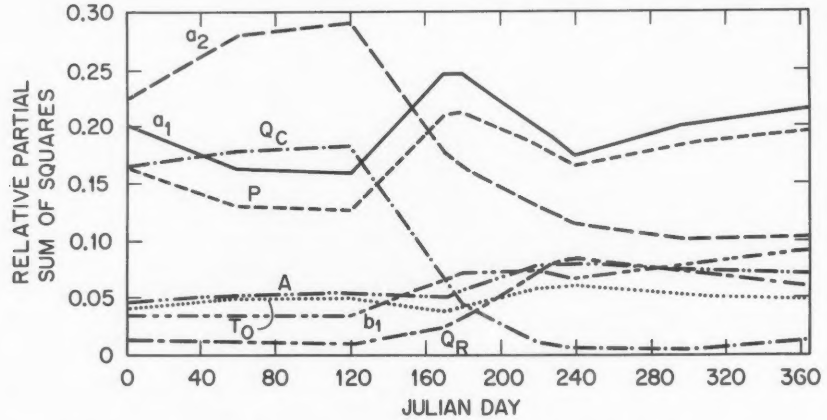

FIG. 4. Temporal variation in parameter importance as measured by the relative partial sum of squares in alewife wet weight accounted for by individual parameters. Results of 150 simulations with 20% coefficients of variation for parameters in age-class I alewife model of seasonal growth not constrained to fit measured growth.

TABLE 4. R^2 statistics in regressions of alewife wet weight vs. parameter values in relation to increased parameter uncertainty (CVs) and diet variability (nc = not calculated).

Diet variability (%)	Parameter coefficient of variation (%)		
	2	10	20
0	0.99	0.99	0.95
25	0.94	0.98	nc
50	0.80	0.98	nc
75	0.65	0.96	nc
100	0.53	0.95	0.94

toporeia, *Mysis*, cladocerans, and copepods. Diet composition was interpolated from enumeration of seasonal samples of age-class III stomach contents (S. Hewett, Center for Limnology, University of Wisconsin, Madison, WI, pers. comm.). The diet proportions determined the caloric value of food consumed by alewife on each day. Expected spatial and temporal heterogeneity in production and distribution of alewife prey argued that estimates of diet composition required by the model were inherently less precise than temperature data. Therefore, values of diet composition for age-class III fish were varied in combination with the three levels of parameter uncertainty (CVs) in repeated simulations of alewife growth.

Variability in diet composition was introduced by randomly increasing or decreasing the fraction of the daily diet that consisted of *Pontoporeia*. Mean variability was arbitrarily chosen as 25, 50, 75, or 100% of the measured contribution of *Pontoporeia* to the alewife diet. The fractional composition of the other prey items was assigned to the remaining portion of the daily diet according to their measured relative importance.

To describe the relative contribution of parameter uncertainty and diet variability to variation in fish growth, we examined the R^2 statistic that resulted from regression of all parameters, while excluding diet variability, against simulated fish weights. Exclusion of diet variability from the regression analyses meant that the value of R^2 was directly proportional to the variance in predictions attributed solely to parameter variation; diet variability explained no more than $1.0 - R^2$ of the remaining variance. For a specific level of parameter variation, the R^2 value should decrease with increasing variation in diet composition. The pattern of change in the R^2 values in relation to diet and parameter variation indicated the conditions where knowing model inputs was more important than precisely estimating model parameters and vice versa.

There was a small decrease in the R^2 values with increased parameter variation under conditions of constant diet (Table 4). This resulted from the omission of interaction and nonlinear terms in the regression model. If parameter standard deviations were 2% of their mean values, increased diet variability added more variance to predicted weight. However, even when diet uncertainty was 100% of the nominal values, parameter variation still explained 53% of the variance in predicted fish weight. For 10% CVs on the parameters, increasing diet variation exerted minimal effect on model precision, the R^2 values decreased by only 4% from the zero diet uncertainty case. When the CVs on parameters were 20%, 100% diet uncertainty contributed less than a 2% change in the R^2. These results showed that for ranges of parameter variation that might reasonably be expected, approximate estimates of seasonal diet composition would suffice. With the current model structure, precision in predictions of alewife growth will increase more through refinement of model parameters than through collection and analysis of more stomach contents, with the caveat that as parameter CVs reduce to ~2%, diet uncertainties will contribute increasingly to model imprecision.

Discussion

Results of the error analyses indicate that we can reduce the model (eq. 1) to a size- and temperature-dependent model of consumption without major loss of predictive power. The IPP and error analyses consistently ranked parameters that determine rates of consumption as most important. These results are generally similar to the findings of Kerr and Dickie (1985). Majkowski and Waiwood (1981) and Stewart et al. (1983) also demonstrated the sensitivity of fish growth models to consumption and respiration parameters, especially if those parameters determine allometric functions.

In the models we analyzed, the formulation of respiration rate was largely independent of terms for consumption, egestion, and excretion (Table 1). The secondary importance of respiration rate in simulated fish growth resulted from the estimation of maximum respiration rate as a power function of fish weight and the nonlinear dependence of that rate on water temperature.

Regardless of the detail in process formulation for specific applications (e.g. Table 1), rates of egestion and excretion were ultimately calculated as a fraction of consumption. The effects of parameters that determined these losses thus depended upon rates of consumption. Therefore, egestion and excretion parameters could not contribute more to prediction uncertainty than the parameters that determined consumption.

The bioenergetics models have provided realistic forecasts of the production dynamics of fishes. Therefore, the results of our analyses can be used to guide further research into understanding the physiological ecology of these organisms. Experimental efforts should focus on better characterization of the effects of temperature (T_0, T_m, Q_C, Q_R) and fish size on rates of consumption (a_1, b_1) and respiration (a_2, b_2). To forecast growth more precisely, better estimates of consumption relative to food availability are needed to refine estimates of P. For purposes of prediction, detailed measurement of egestion and excretion rates (Elliott 1976) appear unnecessary. Representation of these processes as simple fractions of consumption rate seems adequate (Kitchell and Breck 1980). A recent modification of the alewife model includes simplification of the egestion and excretion formulations consistent with the results of our error analyses (D. Stewart, Center for Limnology, University of Wisconsin, Madison, WI, pers. comm.). These refinements and simplifications pertain to use of the model for purposes of forecasting. However, the basic model also serves as a set of operational hypotheses that summarize the current understanding of the growth dynamics of fishes. From this perspective, greater biological detail in formulation of individual growth processes will be valuable.

For fishes in nature, the fraction of the maximum consumption rate realized at any particular time, P in the model vernacular, is influenced by the history of consumption and the immediate availability of prey. It will be difficult to measure P accurately for fish species under nonlaboratory conditions. In addition, P will most likely vary through time. For example, Rice et al. (1983) produced a seasonal pattern of P values hypothesized to reflect food availability for largemouth bass in a heterogeneous thermal environment. Rice and Cochran (1984) determined that three seasonal adjustments of the P value were required to simulate growth of largemouth bass for Lake Rebecca, Minnesota. Disaggregation of the ecological complexity implied by P appears warranted in future model development, even though this will probably lead to an increase in the number of model parameters.

Results of the error analysis of the alewife model support the contention of Kitchell et al. (1977) that the bioenergetics model is a more precise estimator of fish consumption rate, given measurements of growth, than an estimator of growth, given initial conditions and thermal history. In particular model applications, consumption is estimated in a curve-fitting exercise that uses P as the sole independent variable. Other parameters contribute to variability in estimates of consumption during periods of seasonal maximum feeding, yet the possible values that can be assumed by these parameters are constrained by the requirement that simulated growth must agree with measured growth on the dates of observation. Resulting estimates of P have the desired property that they force the model to agree with data. However, the curve fitting shifts attention to the ecological realism of P estimates. Given the expected temporal variation in fish feeding (Rice et al. 1983), a mean value of P might carry little information concerning patterns of realized consumption in aquatic systems. Thus, it is highly doubtful that a meaningful P value can be measured with a coefficient of variation of 10%. Yet, the results shown in Fig. 1 indicate that even 10% variation in the parameters, where P contributes most of the impact, can generate highly imprecise estimates of growth.

The results of the sensitivity analyses may be useful for determining appropriate applications of the bioenergetics models for purposes of management. The models appear adequate for predicting fish growth if consumption rates can be accurately measured. As uncertainties concerning fish feeding increase, use of these models to forecast fish growth becomes more tenuous. Perhaps more credible use of the models lies in fitting observed patterns of fish growth to estimate rates of consumption (Rice and Cochran 1984). This removes the potential problems associated with unreliable estimates of P. With sufficient sampling, fish growth can be measured to desired degrees of accuracy and precision; however, predator impact on prey populations remains difficult, if not impossible, to accurately quantify. Applications of this type may provide realistic estimates of the impact of fish growth on available prey stocks for use in designing harvesting and stocking programs (Stewart et al. 1981).

Results of the two approaches to evaluating perch growth in light of parameter variability may argue for the simple individual parameter perturbation method used by Kitchell et al. (1977). Parameter rankings were similar in both analyses, and the IPP method required only 42 simulations. Each error analysis used 150 simulations for each degree of parameter variation. However, to examine the effects of possible parameter interactions in a rigorous fashion, the IPP method requires 2^{21} (= 2 097 152) simulations. Results of even these 2 million simulations would be valid only for the two levels of parameter perturbations (e.g. ±10%). The stratified random sample guarantees thorough sampling over a continuous range across the entire parameter space in considerably fewer simulations (Iman and Conover 1980). Error analysis also facilitates evaluation of multiple model outputs from the same series of simulations. For example, the temporal variation in parameter ranking during the course of simulations identified by the error analysis would not be as easily determined in the individual parameter perturbation experiments. In addition, the quantification of nonlinear effects and parameter interactions can be more readily accomplished through error analysis.

The dominance of the consumption term in overall behavior of the fish growth models might explain the similarity in ranking of parameters by IPP and error analysis. If the sensitivity of growth to parameter variation is nearly linear, the IPP method will generate accurate estimates of the true partial derivatives. The high values of R^2 and the similarities in parameter ranking across all three levels of variation (Table 2) attest to the linearity of response of predicted growth to parameter variation. A potential weakness of the IPP method lies in the absence of a convenient metric that points out departures from linearity and subsequent inaccuracies in estimating the partial derivatives. To determine departures from linearity, the IPP method requires repetition for at least three magnitudes of parameter variation, with associated increases in computational demands.

The parameter manipulations in IPP do not require distributions to be specified, although IPP implies uniform distributions for model parameters. That is, parameter values are equally likely to be 10% greater or 10% less than the expected values. The uniform distribution equates with the state of minimum information. The methods we have used require additional information concerning parameter distributions, and this can be a drawback. In our analyses, all distributions were assumed normal. To test the effects of this assumption on the analyses, we recalculated the rank order of parameters for the perch model using uniform distributions with ranges defined as ±10% of the mean values. Use of uniform distributions failed to change the order of importance for the top four parameters (Table 2), but T_0 replaced b_2 as the fifth ranked parameter. The b_2 parameter decreased to ninth in rank. These differences in rank, although small, demonstrated that results of the error analysis can be influenced by the underlying parameter distributions. However, it has been our experience in examining a variety of ecological models that the model sensitivities are affected more by differences in parameter means and variances. This is because distributions with equal mean and variance differ primarily in the frequency of extreme values. The probability of sampling jointly from extreme values decreases as the number of model parameters increases. While the requirement of additional information may discourage the use of these methods, the relative ease of examining the implications of different distributions should encourage the use of error analysis.

Prediction errors can result from uncertainties associated with external model inputs in addition to parameter variation. Although, for the alewife model, 10% variation in parameter values very nearly concealed variation in diet proportions. The caloric values (calories per gram wet weight) of the four prey were 1100 for *Mysis*, 1000 for *Pontoporeia*, 550 for copepods, and 400 for cladocerans. Thus, even though prey caloric values differed as much as nearly threefold, the effects of diet uncertainty failed to outweigh the contribution of parameter variation in predicting the growth of age-class III alewife. The results are necessarily specific to the details of the model, its parameters, and diet structure. The main point is that the methods of error analysis facilitate evaluating the relative importance of internal parameter variation versus uncertainty in model inputs.

Independent of the sophistication of the methods chosen, sensitivity analyses should be regarded as a necessary step in development and application of models in ecology. In some instances, simple inspection of model formulations will point out sensitive parameters (e.g. exponents). If the model is linear and parameter ranges are well known, IPP may suffice. As the number of parameters and model nonlinearities increase, we argue that the methods of error analysis, as applied here to the fish models, are efficient tools for quantification of model sensitivities.

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Effect of Aroclor 1254 and Mirex on Estradiol-Induced Vitellogenin Production in Juvenile Rainbow Trout (*Salmo gairdneri*)

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A rapid sensitive assay for vitellogenin using rocket immunoelectrophoresis was developed in juvenile rainbow trout (*Salmo gairdneri*) induced with 17β-estradiol. The assay detected vitellogenin serum levels as low as 0.05 mg/mL. Significant reduction of vitellogenin levels were detected in rainbow trout fed for 6 mo on diets contaminated with Aroclor 1254, Mirex, or a mixture of Aroclor 1254 and Mirex.

On a mis au point un test sensible et rapide faisant appel à l'immunoélectrophorèse de type Laurell, pour déterminer chez de jeunes truites arc-en-ciel (*Salmo gairdneri*) la production de vitellogénine provoquée par l'injection de 17β-estradiol. Le test a permis de déceler dans le sérum des concentrations de vitellogénine aussi faibles que 0,05 mg/mL. On a observé une diminution importante des concentrations de vitellogénine chez des truites arc-en-ciel auxquelles on avait donné pendant une période de six mois de la nourriture contaminée par de l'Arochlor 1254, du Mirex ou un mélange d'Arochlor 1254 et de Mirex.

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In most, if not all, oviparous vertebrates the synthesis of vitellogenin (VG), the precursor protein of the yolk, is under the modulation of estrogen (Deeley et al. 1977; Tata and Smith 1979; Chen 1983). VG is synthesized in the liver, secreted into the vascular system, and deposited in the oocytes as lipovitellin and phosvitin. Unlike ovalbumin synthesis in the avian oviduct (Oka and Schimke 1969) or casein synthesis in the mammary glands (Mehta and Banerjee 1975), which require cytodifferentiation, estrogen-induced VG synthesis in the liver is independent of hepatocyte cell division. Males, which normally do not produce VG, can readily be induced to synthesize VG by exogenous 17β-estradiol, and hence, provide an excellent model for gene induction studies (Tata and Smith 1979; Chen 1983).

In recent years, there has been increasing concern as to the potential health effects of a number of persistent nonvolatile halogenated hydrocarbons (i.e. PCB, DDT, dioxin). This class of chemicals are hepatotoxic and have been associated with reproductive dysfunction in a wide variety of animals such as birds, rodents, primates, and fish (Safe 1984). Our objectives were to develop an assay for VG in juvenile rainbow trout (*Salmo gairdneri*) induced with 17β-estradiol and to study the effects of dietary exposure to Aroclor 1254 (PCB) and Mirex on vitellogenesis.

Materials and Methods

Juvenile rainbow trout (30–50 g) were purchased from Spring Valley Trout Farm (New Delhi, Ont.). The fish were maintained in the laboratory under a 12 h light : 12 h dark photoperiod regime in continuously running, dechlorinated water at 15°C. The fish were maintained in the laboratory 30 d before commencement of the experiment. VG synthesis was induced by intraperitoneal injection with 17β-estradiol (Sigma, St. Louis, MO) dissolved in propylene glycol.

Experimental diets were prepared using a dry starter (GRT-76-5) (Martin's Feed Mills, Elmira, Ont.). Aroclor 1254 or Mirex (a purified preparation donated by Dr. Doug Hallett, Canadian Wildlife Service, Ottawa, Ont.) was suspended in corn oil and slowly added to the feed with continuous mixing in a commercial food mixer. Water was added to the dry mixture (30% wt/wt) and the wet diet mixture was pelleted and stored at −20°C until use. An uncontaminated control diet was prepared in the same manner. Therefore, the concentration of the organochlorines used in the studies here are nominal concentrations.

Groups of 40 fish were randomly distributed into seven tanks maintained under identical conditions. The fish were fed twice daily ad libitum for 6 mo with one of the following diets: Aroclor 1254 (3, 30, and 300 μg/g), Mirex (0.05, 5, and 50 μg/g), an Aroclor 1254 − Mirex mixture (30:5 μg/g), and control diet.

Fish were killed with MS-222 (Sandoz Pharmaceutical) and a blood sample was taken by caudal severance. The blood was allowed to clot overnight at 4°C; the separated serum was stored at −20°C until analysis. The experimental bias that sampling stress might cause was tested by placing unanesthesized fish in a dry container for 5 min before killing and as a control other fish in a similar container with water. Fish were killed at 9:00 a.m. and 3:00 p.m. to ascertain whether circadian variability might affect sampling.

Egg yolk granule proteins and lipovitellins of coho salmon (*Oncorhynchus kisutch*) and rainbow trout were prepared as described earlier (Chen 1983). Antiserum serum to each VG was prepared in rabbit as described earlier (Chen 1983) and rendered specific to VG or lipovitellin by absorption with a

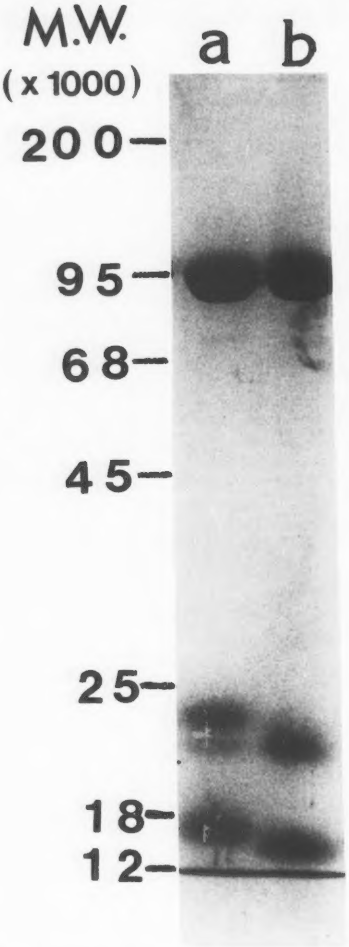

FIG. 1. SDS−polyacrylamide gel (7.5%) electrophoresis of yolk granule proteins from (a) rainbow trout and (b) coho salmon. Protein bands were stained with Coomassie Blue. Molecular weight marker proteins used were myosin (200 000), phosphorylase *b* (95 000), bovine serum albumin (68 000), ovalbumin (45 000), α-chymotrypsinogen (25 000), β-lactoglobulin (18 000) and cytochrome *C* (12 000).

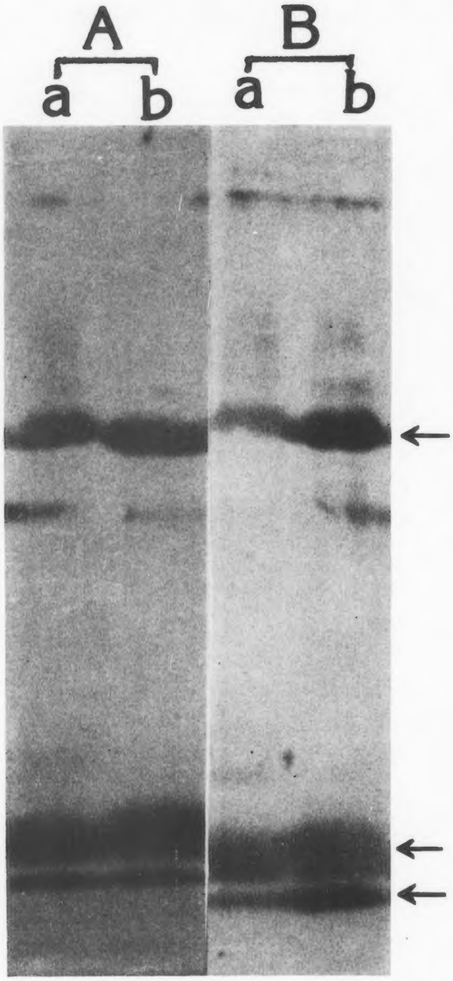

FIG. 2. Determination of the immunological relatedness of yolk granule proteins of (a) rainbow trout and (b) coho salmon by immunoblot analysis. Yolk granule proteins were electrophoresed on a SDS−polyacrylamide gel, electrotransferred to a nitrocellulose filter, reacted with antisera to (A) rainbow trout and (B) coho salmon VG, and then labelled with goat antirabbit IgG horse radish peroxidase conjugate. Arrows indicate lipovitellin and phosvitin.

mixture of acetone powder of the serum and liver extract of control male fish.

SDS−polyacrylamide gel electrophoresis was performed under conditions described by Chen et al. (1978). Immunoblot analysis was carried out following the method described by Towbin et al. (1979) except that the blocking process was done in 0.05 *M* Tris−HCl (pH 7.5) − 0.5 *M* NaCl buffer containing 3% defatted dry milk.

Rocket immunoelectrophoresis was conducted with a 1.5-mm-thick slab of 1% agarose on 0.05 *M* Tris−citrate buffer (pH 8.3) containing 0.1 or 0.05% antilipovitellin serum of rainbow trout. Serum samples were diluted in a Tris−HCl buffer (0.05 *M*, pH 8.3) containinig 0.4 *M* NaCl and 1 m*M* phenyl−methyl−sulfonyl−floride (PMSF), applied into 3-mm sample wells, and were electrophoresed at 130 V for 12−14 h at 4°C. Known amounts of lipovitellin (0.5−12 μg/well) were also included in each electrophoresis run in order to establish a standard curve. The height of each rocket was measured after staining with Coomassie Blue, and the corresponding amount of lipovitellin equivalents in each serum sample was read directly from the standard curve.

Results

The protein patterns of rainbow trout and coho salmon yolk granule proteins were analyzed on 7.5 SDS−polyacrylamide gels (Fig. 1). In both samples, three polypeptides were observed: one comigrating with phosphorylase *b* and the other two migrating slightly slower than the dye front. The molecular weights of these polypeptides from rainbow trout yolk granules

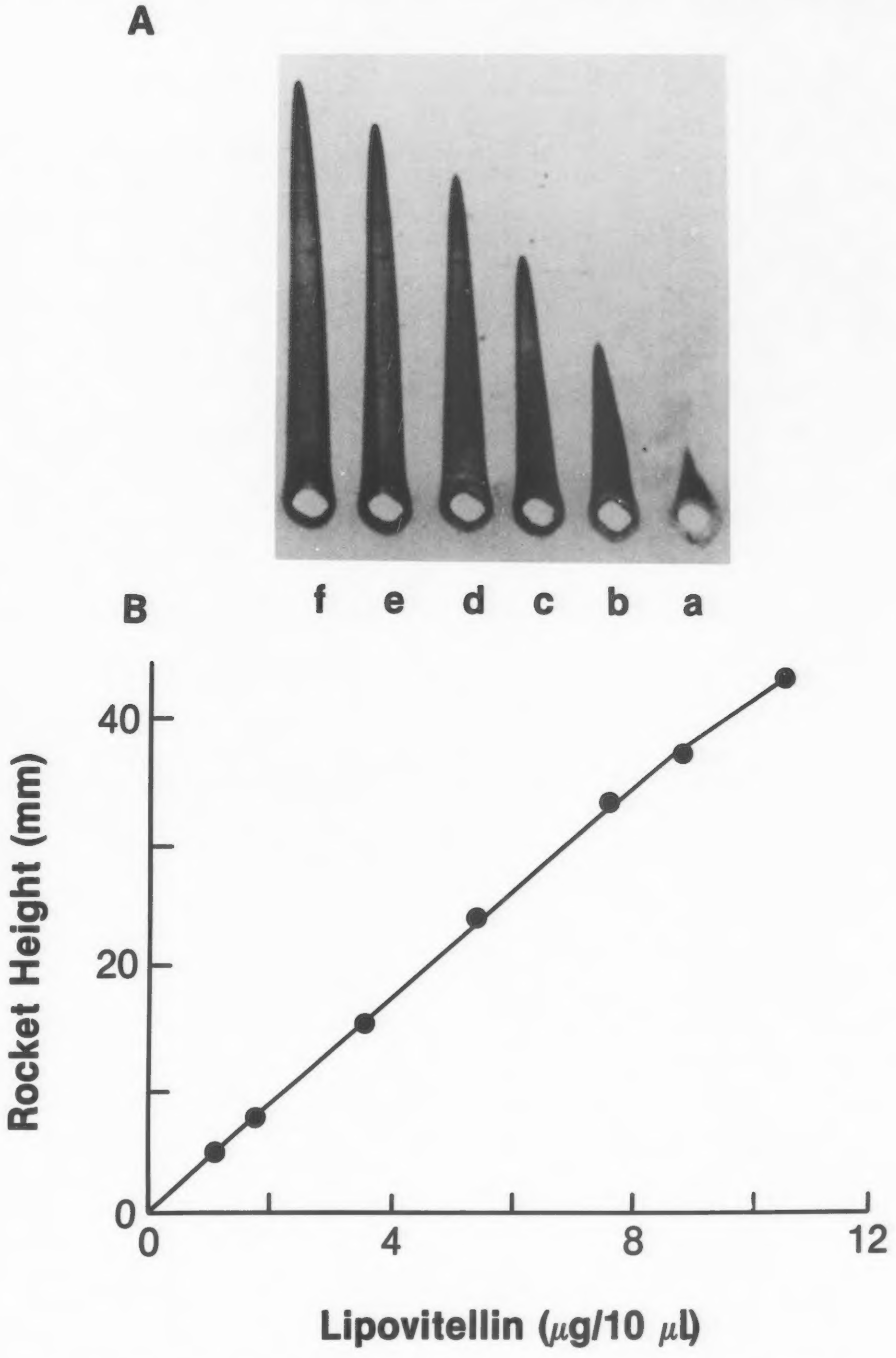

FIG. 3. Quantitative measurement of lipovitellin by rocket immunoelectrophoresis carried out in a 1.5-mm-thick slab agarose gel (1.0%), prepared in 0.05 *M* Tris−citrate buffer (pH 8.3), containing 0.05% anti-VG serum of rainbow trout. (A) Increasing amount of lipovitellin in each sample well was electrophoresed at 40 V overnight at 4°C; (B) linear relationship between the peak height and the amount of lipovitellin in each well.

TABLE 1. Effect of Aroclor and/or Mirex on serum VG levels (* not significant using Student's t-test, $P < 0.05$).

17β-Estradiol (μg/100 g) body weight)	VG present in serum (mg/mL ± SD)							
		Aroclor 1254 (μg/g)			Mirex (μg/g)			Aroclor 1254 − Mirex (μg/g), 30:5
	Control	3	30	300	0.5	5	50	
80	5.06±0.45	2.00±0.86	1.12±0.27	1.41±0.17	3.96±0.62	2.20±0.51	1.10±0.48	1.82±0.30
20	2.72±0.54	1.95±0.40	1.50±0.23	1.27±0.23	2.51±0.56*	1.71±0.35	1.54±0.28	1.24±0.42

NOTE: Groups of fish were fed diets contaminated with known quantities of chemicals indicated for a period of 6 mo. Serum Samples were collected 6 d following treatment with 17β-estradiol. A group of 20 fish was used per treatment.

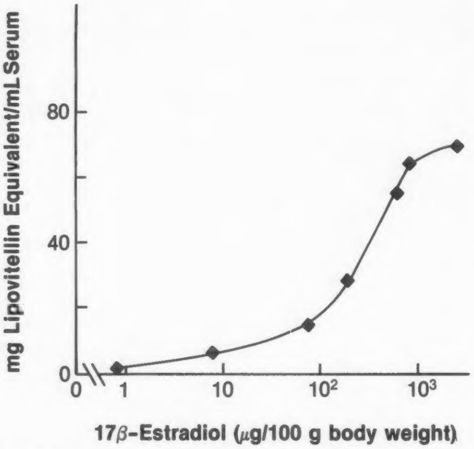

FIG. 4. Dose−response relationship of the accumulation of VG induced by 17β-estradiol. Serum samples were collected from fish (30−50 g) at 6 d after treatment with 17β-estradiol. The content of VG in each serum sample was determined by rocket immunoelectrophoresis. Each data point is an average from 10 fish.

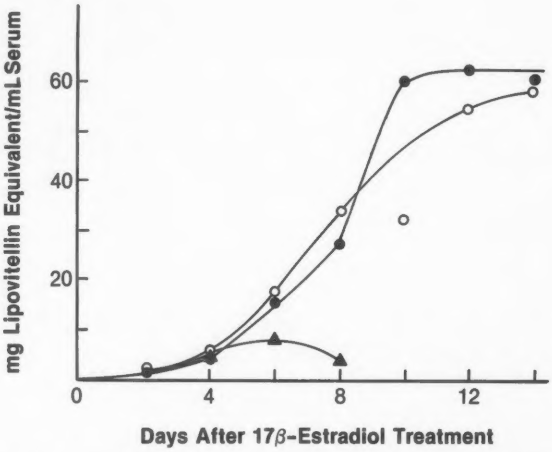

FIG. 5. Accumulation of VG in the serum of rainbow trout following 17β-estradiol treatment. Fish of 30−50 g were treated with 17β-estradiol as indicated, and the levels of VG in the serum samples were determined by rocket immunoelectrophoresis. ▲, 80 μg 17β-estradiol/100 g body weight; ○, 600 μg 17β-estradiol/100 g body weight; ●, 800 μg 17β-estradiol/100 g body weight. Each data point is an average from 10 fish.

were estimated on SDS−polyacrylamide gels to be 95 000, 24 000, and 17 000, respectively. The 95 000 and 24 000 polypeptides have been shown to be heavy chain and light chain lipovitellin and the 17 000 polypeptide phosvitin (Fig. 1a; Chen 1983). The close relationship of rainbow trout and coho salmon yolk granule proteins were determined by immunoblot analysis and Ouchterlony immunodiffusion. Antibody raised against rainbow trout VG reacted specifically with the yolk granule protein of coho salmon and vice versa (Fig. 2). This finding was confirmed by Ouchterlony immunodiffusion where a continuous immunoprecipitation arc was found between samples of both yolk granule proteins.

Different dilutions of antiserum to rainbow trout VG were incorporated into agarose for rocket immunoelectrophoresis. When a concentration of 0.05% antiserum was used, the height of the precipitin peak was directly proportional to the amount of purified lipovitellin present in the sample (in the range of 0.5−8 μg/10 μL per sample) (Fig. 3).

Using the quantitative rocket immunoelectrophoresis, a dose−response relationship of the accumulation of VG in the serum of juvenile rainbow trout in response to exogenous 17β-estradiol was determined (Fig. 4). 17β-Estradiol at the concentration of 2 μg/100 g body weight induced detectable levels of VG in the serum. Maximum induction of VG in the serum was achieved at the dose of 200 μg 17β-estradiol/100 g body weight. The time course for the accumulation of VG in serum in response to 17β-estradiol in vivo was determined. At the doses of 20−80 μg 17β-estradiol/100 g body weight, maximal accumulation of serum VG was reached at day 6 following hormone treatment (Fig. 5). Physical stress caused during sampling or time of the day did not affect the level of VG present in the serum. Therefore, for routine assay of the induction of VG synthesis in vivo, a dose of 20 and 80 μg 17β-estradiol/100 g body weight was used and the serum samples collected at day 6 posthormone treatment.

To investigate the effect of halogenated hydrocarbons on the induction of VG synthesis in rainbow trout, groups of juvenile fish were exposed to Aroclor 1254 and/or Mirex in their diet. Control fish were kept under the same conditions except the diet was not contaminated with chemicals. After feeding for 6 mo, both control and experimental animals were treated with 17β-estradiol at the concentrations of 20 and 80 μg/100 g body weight and the levels of serum VG determined. Aroclor 1254, Mirex, and mixtures of Aroclor 1254 and Mirex significantly suppressed the level of VG induced by 17β-estradiol (Table 1).

Discussion

We developed a rapid sensitive assay for VG in juvenile rainbow trout induced with 17β-estradiol. The rocket immunoelectrophoresis method detected VG levels as low as 0.05 mg/mL of serum and gives reliable quantitation of VG in both induced and noninduced fish. Furthermore, only 10 μL of serum sample is required for the assay. VG in teleosts has been measured by other investigators by radioimmunoassay (Idler et al. 1979) and by SDS−polyacrylamide gel electrophoresis (van Bohemen et al. 1982). Although the rocket immunoelectrophoresis method is not as sensitive as radioimmunoassay, it has the advantages of simplicity and does not require preparation of radioactive lipovitellin or VG. On the other hand, the rocket immunoelectrophoresis protocol is more specific and quantitative than the SDS−polyacrylamide electrophoresis method, and is readily adaptable to the processing of large numbers of samples.

The antibody to rainbow trout lipovitellin showed a continuous precipitation arc (line of identity) with coho salmon lipovitellin in the Ouchterlony immunodiffusion assay, indicating immunological homology of these two different lipovitellins. The rainbow trout VG antisera also reacted with coho salmon lipovitellin in the western immunoblot assay. We suggest that our VG assay may be useful in investigating vitellogenesis in a variety of salmonid fishes.

Using the rocket immunoelectrophoresis protocol, a significant decrease in VG synthesis was seen in rainbow trout fed diets contaminated with Aroclor 1254, Mirex, and/or a mixture of Aroclor 1254 and Mirex. As yet, the mechanisms by which halogenated hydrocarbons exert reproductive toxicity are unknown, but they may be related to altered steroid metabolism (Safe 1984). We hypothesize that mixed-function oxidase induction which is associated with halogenated hydrocarbons may elevate estradiol catabolism, thus decreasing VG levels. Similarly, PCB and Mirex are hepatic toxins in fish as evidenced by hepatomegaly and histopathology (Leatherland et al. 1979) which may lower VG synthesis at the organ level.

As a result of man's manufacturing and agricultural activities, feral fish are exposed to an environmental cocktail of persistent nonvolatile halogenated hydrocarbons (Norstrom et al. 1978; Sullivan et al. 1983). The positive correlation of this class of chemicals with reproductive dysfunction in birds, rodents, mink, and primates (Safe 1984) suggests that similar problems likely occur in exposed fishes. We suggest that investigations of environmental xenobiotics which affect vitellogenesis may provide a useful probe in the screening of chemicals and/or mixtures of chemicals which may affect reproduction in fishes. In addition, the elucidation of the mechanisms of VG promises to provide strategies for the induction of reproduction in fishes for aquacultural purposes.

Acknowledgments

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Analyzing Catch–Effort Data Allowing for Randomness in the Catching Process

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For many fisheries the only reliable data is a (bivariate) time series of catches and efforts. Most existing methods of analyzing such data implicitly assume that the main source of randomness is in the dynamics of the population, while ignoring randomness in the catching process. The assumption of a *deterministic* catch production function (usually of the Schaefer form $C = qEX$) must be contrary to the experience of almost everyone who has ever gone fishing. In this paper a *stochastic* catch model coupled with a deterministic dynamic model is used in the analysis of catch–effort data and shown to give very plausible results. Estimates (with confidence intervals) of catchability, maximum sustainable yield, and other dynamic model parameters are obtained numerically by the method of maximum likelihood. The incorporation of stochastic dynamics with the stochastic catch model is difficult.

Pour de nombreuses pêches, les seules données fiables sont une série chronologique (à deux variables) de prises et d'efforts de pêche. La plupart des méthodes utilisées actuellement pour analyser ces données présument implicitement que la principale source de hasard se trouve dans la dynamique de la population, mais elles ne tiennent pas compte du caractère aléatoire de la méthode de capture. L'hypothèse d'une fonction *déterminée* de la production par prise (généralement de la forme Schaefer $C = qEX$) doit être contraire à l'expérience de presque tous ceux qui sont déjà allés à la pêche. Dans cet article, on se sert d'un modèle de prises *stochastique* associé à un modèle dynamique déterminé pour analyser les données sur l'effort de capture et l'on montre que ce modèle donne des résultats très vraisemblables. On se sert de la méthode du maximum de vraisemblance pour donner une estimation (avec intervalles de confiance) de la possibilité de capture, du rendement maximal soutenu et d'autres paramètres du modèle dynamique. Il est difficile d'intégrer la dynamique stochastique au modèle stochastique des prises.

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For many fisheries the only reliable data available for management purposes is in the form of a (bivariate) time series of annual catches and annual aggregated efforts. Various methods of analyzing such data have been proposed. Stock production models based on the logistic differential equation or some relative of it have been used in the analysis of catch–effort data by Schaefer (1954), Pella and Tomlinson (1969), Schnute (1977), and others. In all the above methods the mathematical model describing the population dynamics is manipulated to obtain a predictive equation in observable quantities (catches and efforts), and the parameters of the model are then estimated by ordinary least-squares regression.

A similar approach is used in the method of Deriso (1980) although the underlying model for the population dynamics is much more sophisticated allowing for growth, age structure, seasonal harvesting, and continuous recruitment. From the population model, a predictive equation relating catches and efforts is derived which is nonlinear in the model parameters. Nonlinear least-squares regression is used to estimate the many parameters.

Regression methods are also used in the methods of Gulland (1961) and Fox (1970). These methods eschew the specification of an underlying dynamic model in favor of a statistically more pragmatic approach of developing a *statistically* simple model relating the output catch series to the input effort series. Specifically they involve the linear regression of catch-per-unit-effort (or the logarithm of it) on the average effort over the past several years. This "black box" modelling approach is along the lines of much econometric work, and a natural extension would be to use more sophisticated "black box" methods employed in that discipline such as the Box–Jenkins transfer function models (Box and Jenkins 1976).

In all of these methods, based on regression, noise or error is included in the most expedient place. In the stock–production models (whether of the Schaefer or Deriso form) this is an additive error term tacked onto the deterministically derived predictive equation in observable catches and efforts. The implication of this is that the noise occurs either additively or multiplicatively in the catch per unit effort (CPUE). If one regards CPUE as a proxy for population size, one sees that these methods make the not unreasonable implicit assumption that *noise is occurring in the population dynamics*. Noise, or randomness, in the catching process is ignored. Indeed all of the stock–production models above explicitly assume the *deterministic* Schaefer production function model $C_t = qE_tB_t$ relating catch to effort and biomass.

While undoubtedly much randomness occurs in the dynamics of a natural population, it is also undeniable that much randomness occurs in the process of catching fish. Anyone who has ever gone fishing knows that fixed levels of effort input can result in highly variable catch outputs. There is no a priori reason for supposing that the randomness in the catching pro-

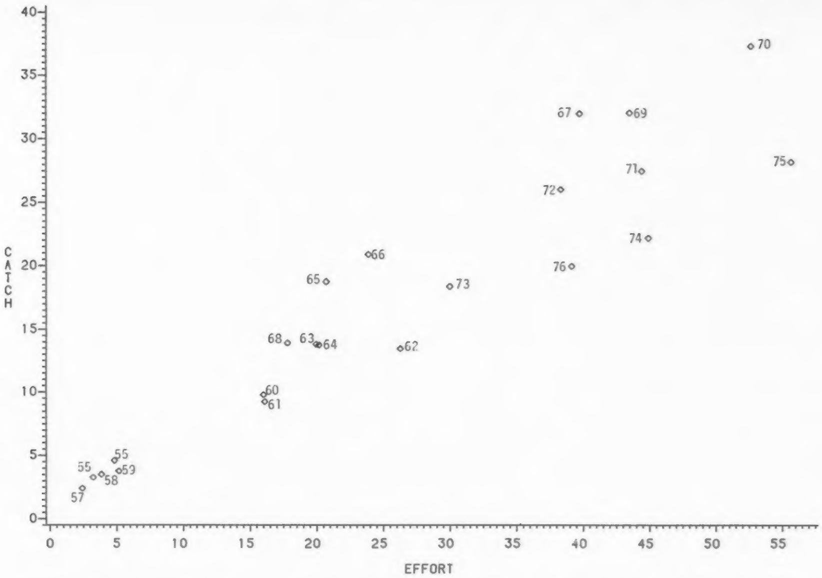

FIG. 1. Total annual catch versus total annual effort for North Atlantic redfish for ICNAF division 3P for the years 1955–76. Units of catch are thousands of metric tons and units of effort are thousands of hours.

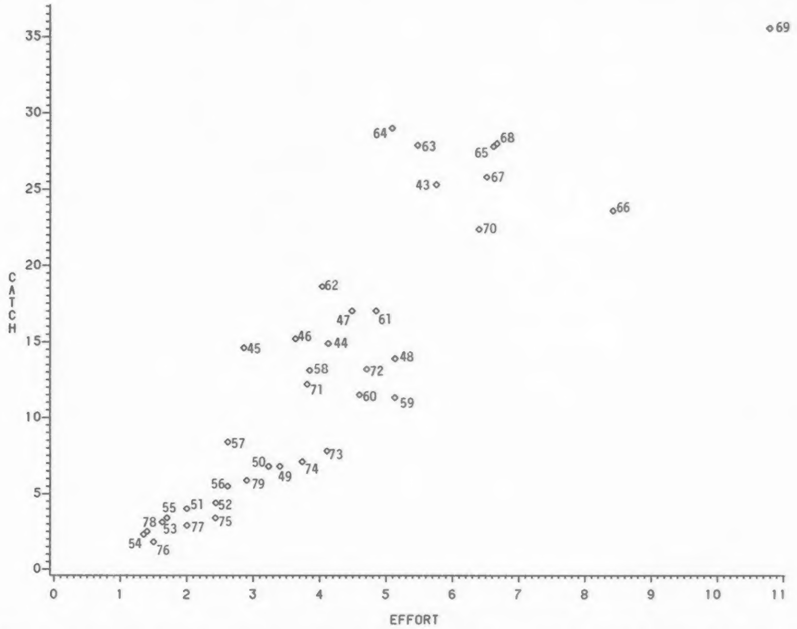

FIG. 2. Total annual catch versus total annual effort for New England yellowtail flounder for the years 1943–79. Units of catch are thousands of metric tons and units of effort are thousands of days.

cess is any less significant than that in the population dynamics.

The purpose of this paper is to present a method of analysis of catch–effort data based on an explicit stochastic model for the catching process. In order to be able to carry out the analysis it was necessary to assume that the dynamics of the population are deterministic. Ideally, a method of analysis that explicitly recognizes the randomness both in the catch process and in the population dynamics would be preferred. Unfortunately there are serious statistical difficulties associated with this. The methods of Gulland and Fox, which make no explicit assumptions about the population dynamics or the catching process, are robust enough to allow for noise from either source, the catch variable occurring only on the left-hand side of the regression equations employed.

The Model and Estimation of Model Parameters

Typical plots of catch versus effort (see Fig. 1 and 2) reveal a tendency not only for the occurrence of higher levels of catch at higher levels of effort but also for greater variability in catch at higher levels of effort. This is exactly what one would expect if one considers randomness to occur in the catching process. To see this, consider a highly simplified situation in which one goes fishing for the same length of time for each of E days. Suppose that the catch, c_i, on day i is a random variable with mean μ and variance σ^2. From elementary probability theory it follows that he total catch over E days ($= c_1 + c_2 + \ldots + c_E$) will be a random variable with mean $E\mu$ and variance (if catches on separate days are independent) equal to $E\sigma^2$. Thus, mean catch and variance of catch will both increase linearly with effort E. A glance at Fig. 1 and 2 would suggest that such a simple model might explain much of the observed variation in catches for these two fisheries.

Appealing as such a simple model might be, it ignores any dependence of the catch on the size of the fish stock. An alternative model with the similar features to the model above is that the total catch C_t in year t is a *Poisson random variable* with mean $\lambda = qE_tX_t$, where E_t is the *total effort in year t*, X_t is the *population size* at the start of the fishing season in year t, and q is a constant which, following previous usage, we shall call the *catchability coefficient*, i.e. C_t is a random variable (r.v.) with probability mass function

$$(1) \quad f(C_t) = \frac{e^{-qE_tX_t}(qE_tX_t)^{C_t}}{C_t!} \quad C_t = 0, 1, 2, \ldots$$

This Poisson model can be derived from a stochastic model of the fishing process under certain simplifying assumptions (see Appendix 1).

From the well-known properties of the Poisson distribution it follows that under this model

$$(2) \quad \begin{aligned} E(C_t|X_t) &= qE_tX_t \\ \operatorname{var}(C_t|X_t) &= qE_tX_t. \end{aligned}$$

Thus this model also has the features, observed in the data, of greater mean catch and greater variability in catch at higher levels of effort. Furthermore, the catch depends on the stock size, specifically with the Schaefer production function holding in terms of expected catch.

The Poisson distribution is a distribution on the integers, and thus the variable C_t should be dimensionless. It is this dimensionless aspect of the Poisson r.v. that allows for its curious characteristic of having equal mean and variance. Thus, C_t should be measured in numbers of fish or numbers of schools of fish, or something similar, for the above model to hold, and indeed in the derivation in Appendix 1 we make just such an assumption. Catch data, however, are usually given in biomass units (e.g. metric tons). If we now suppose that C_t is measured in biomass units and population size X_t measured likewise, then our basic Poisson model above should be that $m^{-1}C_t$ has a Poisson distribution with mean $\lambda = qE_tm^{-1}X_t$, where m is a parameter representing the biomass of a single fish or school of fish. We could leave the model in this form and attempt to estimate m along with the other parameters of the model. It turns out that the maximum likelihood (ML) estimates of the other parameters are unaffected by m (i.e. by the units in which C_t and X_t are measured) but that standard errors (and confidence intervals from large sample maximum likelihood theory are affected. Furthermore, the ML estimate of m turns out to be related to the greatest common divisor of the catches C_t (measured in biomass units). This does not appear to be particularly useful because this quantity will be highly sensitive to small errors in measuring or recording the catch.

Rather than following this route and foresaking the possibility of obtaining confidence intervals for our parameter estimates, we shall adopt a different model which we can regard either as an approximation to the above Poisson model or as the basic model in its own right. Specifically, if C_t and X_t are measured in biomass units we shall assume that

$$(3) \quad \sqrt{C_t} \sim N(\sqrt{qE_tX_t}, \sigma^2)$$

i.e. that the square-root of the catch is normally distributed with mean $\sqrt{qE_tX_t}$ and variance σ^2. For this model a simultaneous change in the units of C_t and X_t results only in a change in the value of the variance parameter σ^2. It follows from this fact that confidence intervals for the model parameters (apart from σ^2) will be scale-invariant.

The square-root transformation is well known as a variance-stabilizing transformation for the Poisson distribution (see e.g. Rao 1965, p. 357). It is also known to have a normalizing effect for this distribution. Thus, if we so wish, we can regard the above root-normal model as being an approximation to the Poisson model. Since ultimately all models are approximations, it does not really matter how we view the root-normal model. The only real validation for any model can be obtained by seeing how well it fits observed data, and in this respect the root-normal model performs creditably. Furthermore, ML point estimates of the model parameters obtained using the root-normal model appear to be very close to those obtained using the Poisson model (see Results). The root-normal model relating catch and effort has been used by Kirkwood (1981).

For the root-normal model it can be shown that

$$(4) \quad \begin{aligned} E(C_t) &= qE_tX_t + \sigma^2 \\ \operatorname{var}(C_t) &= 4\sigma^2(qE_tX_t + \sigma^2). \end{aligned}$$

Thus the root-normal model has the desired features of increasing expected catch and increasing variance of catch with increasing effort. Indeed as with the Poisson model the variance of C_t is proportional to its expected value.

We now consider parameter estimation by the method of maximum likelihood (see e.g. Cox and Hinkley, 1974). Given an observed sequence of catches and efforts $\{(C_t, E_t)\}_{t=1,2,\ldots,n}$, the likelihood function is

$$(5) \quad L = k(\sigma^2)^{-n/2} \exp\left\{-\frac{1}{2\sigma^2}\sum_{t=1}^{n}(\sqrt{C_t} - \sqrt{qE_tX_t})^2\right\}$$

where k is a constant. Note that the likelihood depends on the *unobserved* variables X_t, and thus we cannot simply maximize L over q and σ^2 to obtain ML estimates. However, if we assume a *deterministic model for the population dynamics*

$$(6) \quad X_{t+1} = F(S_t; \boldsymbol{\theta})$$

(where $S_t = X_t - C_t$ is the *escapement* and $\boldsymbol{\theta}$ is a vector of parameters of the dynamic model), and an *initial value* X_1 for the population size, then we can determine $X_2, X_3, \ldots, X_n$ recursively as functions of X_1, $\boldsymbol{\theta}$ and the C_t, and thus the likelihood in (5) can be expressed as a function of the parameters q, σ^2,

$\boldsymbol{\theta}$, and X_1 (and of course the data (C_t, E_t)).

For example, we could use the *Ricker model* (Ricker 1954) for the population dynamics

$$(7) \quad X_{t+1} = \alpha S_t \exp(-\beta S_t).$$

Under this model

$$X_2 = \alpha(X_1 - C_1)\exp(-\beta(X_1 - C_1))$$

which is a function of α, β, and X_1; and

$$X_3 = \alpha(X_2 - C_2)\exp(-\beta(X_2 - C_2)),$$

which can be expressed as a function of α, β, and X_1, since X_2 is a function of these parameters. Similarly, $X_4, \ldots, X_n$ can be expressed as functions of α, β, and X_1. Thus, given values of the parameters α, β, X_1, q, and σ^2, we can compute values of $X_2, X_3, \ldots$ etc., and a corresponding value of the likelihood L in (5). We can then numerically seek those value of the parameters α, β, X_1, q, and σ^2 that maximize the likelihood L.

Instead of doing this directly, we shall simplify the numerical maximization problem by first analytically maximizing the likelihood over σ^2 and q. To do this we look at the log-likelihood

$$(8) \quad \ell(q, \sigma^2, \boldsymbol{\theta}, X_1) = \ln L = -n/2 \ln \sigma^2 - \frac{1}{2\sigma^2} \times \Sigma(\sqrt{C_t} - \sqrt{qE_tX_t})^2 + \text{const.}$$

Now $\partial\ell/\partial\sigma^2 = 0$ when

$$(9) \quad \sigma^2 = \hat{\sigma}^2 = \Sigma(\sqrt{C_i} - \sqrt{qE_iX_i})^2/n$$

and $\partial\ell/\partial q = 0$ when

$$(10) \quad q = \hat{q} = \frac{(\Sigma\sqrt{C_tE_tX_t})^2}{(\Sigma E_tX_t)^2}.$$

The maximized log-likelihood or "concentrated" log-likelihood is

$$(11) \quad \hat{l}(\boldsymbol{\theta}, X_1) = l(\hat{q}, \hat{\sigma}^2, \boldsymbol{\theta}, X_1) = -\frac{n}{2}\Sigma(\sqrt{C_t} - \sqrt{\hat{q}E_tX_t})^2$$

where $\hat{q}$ is given by (10). We now seek to maximize numerically the concentrated likelihood l over the parameters $\boldsymbol{\theta}$ and X_1 subject to the constraints $X_t \geq C_t (t = 2, 3, \ldots, n)$ to obtain the ML estimates of all the parameters. The method of numerical maximization adopted to obtain the results given in the next section was the *simplex algorithm* of Nelder and Mead (1965).

To reduce the number of parameters, another simplification can be considered; if we assume that before harvesting started the population was in equilibrium, then the parameter X_1 can be replaced by $X_e = X_e(\boldsymbol{\theta})$ where X_e is the solution to

$$(12) \quad X = F(X; \boldsymbol{\theta}).$$

With this simplification the concentrated likelihood (11) is a function only of the parameters $\boldsymbol{\theta}$.

For a given set of data, and a given dynamic model $F(S; \boldsymbol{\theta})$, we shall obtain ML estimates of the parameters $\boldsymbol{\theta}$, q, and σ^2 assuming both (i) X_1 a free parameter and (ii) X_1 = equilibrium level, X_e. Furthermore, using the invariance property of ML estimates we shall obtain the ML estimate of the maximum sustainable yield (MSY) for the given dynamic model F. Also when the likelihood function is sufficiently smooth we shall obtain approximate standard errors of these parameter (and MSY) estimates by numerically determining the observed information matrix (the Hessian matrix of second derivatives of l at the maximum) and using asymptotic maximum likelihood theory (see Cox and Hinkley 1974, p. 302).

While approximate 95% confidence intervals of the form

Estimate ± 1.96 × standard error

can easily be calculated (Cox and Hinkley 1974, p. 342), such confidence intervals may well be considerably in error, except for all but the longest data series. The reason for this is that the procedure is based on a quadratic approximation to the likelihood function which, while it holds asymptotically, may be far from accurate for series of finite length. An alternative procedure for obtaining confidence intervals is to use the *maximum likelihood ratio test* procedure (Cox and Hinkley 1974, p. 322). Details of this procedure are given in Appendix 2. This procedure is likely to provide better confidence intervals for shorter series, although it is computationally somewhat more cumbersome.

Before adopting any particular model, we shall examine the residuals to determine the adequacy of the fit.

Results

The method has been applied to two sets of catch–effort data: (a) North Atlantic redfish (*Sebastes marinus*) for ICNAF division 3P and (b) southern New England yellowtail flounder (*Limanda ferruginea*). The redfish data were obtained from Huang and Redlack (1981) and the yellowtail flounder data from McBride et al. (1980).

Since there was no a priori information regarding the appropriate parametric form of the dynamic model, several different forms were used and the results compared in an attempt to identify a satisfactory model (Schnute 1985). The following forms were used.

(i) *The Ricker model* (Ricker 1954):

$$(13) \quad X_{t+1} = S_t \exp\left\{\beta\left(1 - \frac{S_t}{X_e}\right)\right\}.$$

With this parameterization of the Ricker model the parameter X_e represents the unfished equilibrium stock level, while β is a parameter related to the intrinsic growth rate.

(ii) *The logistic model*:

$$(14) \quad X_{t+1} = S_t + \frac{4\alpha}{X_e} \cdot S_t\left(1 - \frac{S_t}{X_e}\right).$$

With this parameterization X_e again represents the unfished equilibrium level, while α represents the MSY obtained by maintaining the escapement at $S = X_e/2$.

(iii) *The Beverton–Holt model* (Beverton and Holt 1957):

$$(15) \quad X_{t+1} = \frac{(1 + \beta X_e)S_t}{1 + \beta S_t}.$$

The parameters β and X_e have similar interpretations to those in the Ricker model.

(iv) *The Cushing log-linear model* (Cushing 1971):

$$(16) \quad X_{t+1} = \alpha S_t^{\beta}.$$

The Ricker and logistic models both exhibit overcompensation, while the Beverton–Holt and Cushing models do not, both being nondecreasing functions. Apart from the Cushing model, the above dynamic models all belong to the class of models considered by Deriso (1980) and Schnute (1985).

TABLE 1. Maximum likelihood estimates (underlined) and (where available) approximate standard errors (in parentheses) and 95% confidence limits (in square brackets) for model parameters for redfish data. Units of σ^2, α, X_e, X_1, and MSY are thousands of metric tons. Units of q are (thousand hours)$^{-1}$, while β is dimensionless.

	Ricker model		Logistic model	
	X_1 free	$X_1 = X_e$	X_1 free	$X_1 = X_e$
$\hat{q}$	$\underline{0.0153}$(0.0008) [0.0093–0.0169]	$\underline{0.0152}$(0.0011) [0.0063–0.0167)	$\underline{0.0131}$	$\underline{0.0114}$
$\hat{\sigma}^2$	$\underline{0.0679}$(0.0233) [0.037–0.154]	$\underline{0.0739}$(0.0243) [0.041–0.157]	$\underline{0.0570}$	$\underline{0.0794}$
$\hat{X}_e$	$\underline{42.34}$(1.43) [40.5–77.5]	$\underline{42.76}$(3.24) [40.2–113.5]	$\underline{50.33}$	$\underline{58.50}$
$\hat{X}_1$	$\underline{50.51}$(7.28) [35.4–99.2]	—	$\underline{54.34}$	—
$\hat{\beta}$	$\underline{1.846}$(0.108) [1.23–2.03]	$\underline{1.805}$(0.183) [1.03–1.98]	—	—
$\hat{\alpha}$	—	—	$\underline{32.58}$	$\underline{30.29}$
$\widehat{\text{MSY}}$	$\underline{34.46}$(2.53)	$\underline{33.51}$(3.60)	$\underline{32.58}$	$\underline{30.29}$
R^2	97.4%	97.0%	98.0%	96.7%

For each model fitted, plots of the residuals (in the $\sqrt{C_t}$ scale) against year t, against E_t, against estimated stock sizes ($\hat{X}_t$), and against "fitted" values $\sqrt{\hat{q}E_t\hat{X}_t}$ were made. If the model is adequate, these plots should approximate those of Gaussian white noise. A value of a coefficient of determination R^2, defined as

$$(17)\quad R^2 = 100\left(1 - \frac{\Sigma(C_t - \hat{C}_t)^2}{\Sigma(C_t - \bar{C}_.)^2}\right)$$

(where $\hat{C}_t = \hat{q}E_t\hat{X}_t + \hat{\sigma}^2$ and $\bar{C}_. = (1/n)\Sigma C_t$), was calculated for each model fitted. The complement of R^2 represents the proportion of total variation in the catch series left unexplained after the effect of the effort series through the model has been removed. As in ordinary regression theory a large value of R^2 indicates that, through the model, much of the variation in catch can be explained by variation in effort.

Whenever the fitted model was adequate the ML estimate of the MSY was obtained. For the logistic model the MSY is represented by the parameter α, but for the Ricker model the MSY is given by

$$(18)\quad S_0 \exp\{\beta(1 - S_0/X_e)\} - S_0$$

where S_0 is the solution to

$$(19)\quad \frac{dF}{dS} = (1 - \beta S/X_e)\exp\{\beta(1 - S/X_e)\} = 1\,.$$

To find the ML estimate of MSY, ML estimates $\hat{\beta}$ and $\hat{X}_e$ were substituted for parameter values in (18) and (19); (19) was then solved numerically and the solution, S_0, substituted in (18).

Asymptotic variances of parameter estimates were obtained by numerically determining the inverse of the observed information matrix as described earlier. Determining the asymptotic variance of the MSY estimate for the Ricker model was more complicated, and details are given in Appendix 3. Confidence intervals for model parameters were determined by the maximum likelihood ratio test procedure (Appendix 2).

Redfish

Following the practice of Huang and Redlack (1981), only the first 17 yr of the redfish data (1955–71) were used to fit the model. Catch predictions for the years 1972–76 were made later using the fitted model and then compared with the actual catches (see Catch Predictions).

For both the Ricker and logistic models the maximization routine converged satisfactorily. Residual plots gave no indication of model inadequacy except for the suggestion of pattern in the time-series plot with $X_1 = X_e$ for the logistic model. For this case a runs test (see e.g. Draper and Smith 1981, p. 157) on the residuals produced a significant result.

For the Beverton–Holt and Cushing models, the maximization routine failed to converge. In repeated iterations it set X_e larger and larger and the slope at X_e smaller and smaller. It appears that a dynamic model that does not allow for overcompensation is inadequate for these data.

Table 1 gives point estimates for the model parameters and for the MSY for both the Ricker and logistic models. Note the high values of R^2 for all the models fitted.

When fitting the logistic model, the likelihood function turned out to be very irregular with spikes, ridges, etc., occurring. This vitiated the use of asymptotic maximum likelihood theory in obtaining variances and confidence intervals for the estimates, since that theory is based on the convergence of the normalized log-likelihood to a smooth form. The reason for the irregularity in the likelihood can be seen by looking at the fitted dynamic model. In both cases the slope $1 - 4\hat{\alpha}/\hat{X}_e$ of the fitted function (14) at $X = \hat{X}_e$ is less than -1, implying an unstable equilibrium. Thus small changes in say X_1 (or in other parameters) can cause considerably changes in the trajectory of the X_t (May 1976) and thus in the likelihood.

For both cases of the Ricker model the log likelihoods appeared smooth, and approximate standard errors of the estimates were obtained by inverting the observed information matrix (Table 1, in parentheses). Approximate 95% confidence intervals for model parameters were obtained by the maximum likelihood ratio method (Appendix 2) and are given in Table 1 beneath the estimates. It turned out that for most parameters the likelihood (maximized over the other parameters) showed a considerable degree of skewness, and thus the confidence intervals obtained were not symmetric and deviated considerably from the form estimate ± 1.96 × standard deviation. An illustration of the likelihood for X_e maximized over the parameters β, X_1, q, and σ^2 is shown in Fig. 3. It should be noted that the estimates and confidence intervals for the various parameters are not independent. For example, with $X_1 = X_e$ the estimates of X_e and q and of X_e and β have quite strong negative correlations (estimated as -0.87 and -0.89, respectively), while the estimates of q and β have a positive correlation (estimated as 0.68).

Since the equilibrium of the fitted Ricker model with X_1 free is stable, it seems reasonable to expect that before fishing started the population would be at or near the equilibrium. We can test this hypothesis (H_0: $X_1 = X_e$) by using the asymptotic distribution of the appropriate maximum likelihood ratio statistic (Cox and Hinkley 1974, p. 322). The observed value of $W = -2\ln\Lambda = 1.38$ yielded an approximate significance level, $p = 0.24$. Thus it appears that the data are compatible with the simplifying assumption that $X_1 = X_e$. Allowing X_1 to be free, however, allows for a somewhat smaller error variance and narrower confidence intervals for the model parameters.

The fitted equilibrium of the logistic model is unstable, and

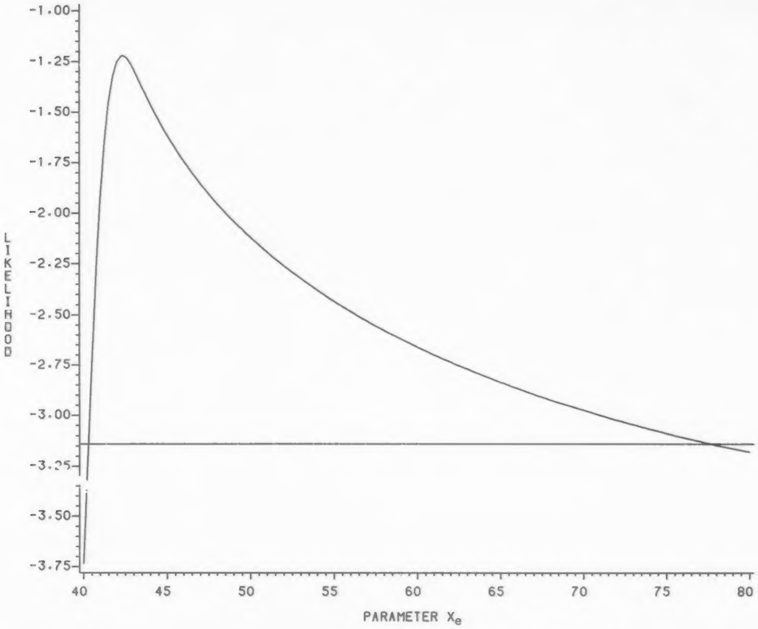

FIG. 3. Log-likelihood, maximized over the parameters β, X_1, q, and σ^2, versus the parameter X_e for the Ricker model with redfish data. The horizontal line is 1.92 ($= 1/2\ \chi^2_{1,\ 0.005}$) units below the maximum; a 95% confidence interval for X_e is given by the set of values of X_e for which the log-likelihood lies above this line (see Appendix 2). Note the high degree of skewness of the log-likelihood.

there is thus no reason to expect similar results would be obtained by starting with X_1 equal to X_e as when starting with X_1 free. This probably explains the poor fit of the logistic model with $X_1 = X_e$. Unfortunately, the irregularity of the likelihood function prevents the use of an asymptotic maximum likelihood ratio test of H_0: $X_1 = X_e$.

It appears that the Ricker model (either with $X_1 = X_e$ or X_1 free) and the logistic model with X_1 free all provide an adequate fit to the data. The estimates of model parameters for the two forms of the Ricker model are very compatible, as might be expected. While the estimate of the unfished equilibrium, X_e, is somewhat different using the logistic model, it is interesting to note that the estimates of the other parameters, and especially of the MSY, are broadly similar to those from the Ricker models. This suggests some robustness in the procedure to the shape of the function F in the dynamic model (14).

From the Ricker model (with X_1 free) we get an estimate of the MSY as 34 500 metric tons (t) with a standard error of 2500 t. The annual catch in the years 1955–76 exceeded 30 000 t only three times and so it could be that the stock was not being fully exploited over that period. However, we shall see in the next section that a somewhat lower estimate of MSY may be more appropriate.

Huang and Redlack (1981) analyzed the same data using methods based upon those of Gulland (1961), Fox (1970), and Schaefer (1954). The methods of Gulland and Fox failed to work on the data (both giving regression lines with positive slope). Schaefer's method gave estimates $\hat{q} = 0.0374$ per thousand hours and $\widehat{\text{MSY}} = 16\ 100$ t. However, the authors were not satisfied with these estimates and, because of the low CPUE observed between 1959 and 1964, made a somewhat arbitrary adjustment by increasing the CPUE for these years by a factor 3/2. This, indeed, produces a better fit and allows Gulland's method to work, giving estimates of MSY between 20 600 and 38 300 t, depending on the number of years used in averaging the effort. The Schaefer method with this adjustment is shown to be quite insensitive to the value of q, and estimates of MSY in the range of 26 300 to 28 000 t for q = 0.014 to 0.034 were obtained. These estimates appear to be somewhat lower than those obtained here.

TABLE 2. Maximum likelihood estimates of model parameters for redfish data using the Poisson catch model (1). Units of α, X_e, and X_1 are thousands of metric tons. Units of q are (thousand hours)$^{-1}$, while β is dimensionless.

	Ricker model		Logistic model	
	X_1 free	$X_1 = X_e$	X_1 free	$X_1 = X_e$
$\hat{q}$	0.0154	0.0153	0.0131	0.0115
$\hat{X}_e$	42.28	42.67	50.27	58.35
$\hat{X}_1$	49.82	—	54.25	—
$\hat{\beta}$	1.846	1.805	—	—
$\hat{\alpha}$	—	—	32.63	30.11

For the sake of comparison between the root-normal and Poisson catch models, ML estimates of model parameters for the Poisson catch model (1) were determined. In this case, of course, the likelihood function has a different form from that in (5). Estimates of parameters are given in Table 2. It can be seen that there is a very close agreement between the results using the root-normal and Poisson models.

TABLE 3. Maximum likelihood estimates of model parameters for yellowtail flounder. Units of σ^2, α, X_e, and X_{-9} are thousands of metric tons. Units of q are (thousand days)$^{-1}$, while β is dimensionless.

	Ricker model		Logistic model	
	X_{-9} free	$X_{-9} = X_e$	X_{-9} free	$X_{-9} = X_e$
$\hat{q}$	0.0822	0.0691	0.0683	0.0658
$\hat{\sigma}^2$	0.2181	0.2542	0.2809	0.3007
$\hat{X}_e$	28.558	36.494	38.691	40.063
$\hat{X}_{-9}$	33.063	—	54.302	—
$\hat{\beta}$	2.402	2.252	—	—
$\hat{\alpha}$	—	—	30.630	30.716
$\widehat{\text{MSY}}$	37.694	42.439	30.630	30.716
R^2	85.2%	83.8%	81.3%	80.1%

Yellowtail Flounder

McBride et al. (1980) gave data on catch and effort in the southern New England yellowtail flounder fisheries for the years 1943–79. They also gave catch data alone for the years 1935–42. Use was made of this preliminary catch data in determining X_1 (in the base year 1943) by iteratively using the dynamic equation (6) with X_{-9} (1935) either regarded as a free parameter or equal to the equilibrium level, X_e.

As with redfish, the maximization routine converged satisfactorily for both the Ricker and logistic models, but failed to do so for the Beverton–Holt and Cushing models. Residual plots for the Ricker model were satisfactory except for the time-series plots. In both cases of the Ricker model, runs tests revealed significantly too few runs. This phenomenon was not present for the logistic fits. However, for the logistic fits, there was some suggestion of greater variance in the residuals at higher levels of X_t, but since thre were few points with low X_t and many with large X_t, this effect could be illusory. Other residual plots for the logistic model were quite satisfactory.

For both models, contour plots of the log-likelihood revealed irregular behavior. Again this is apparently because of the instability of the equilibrium of the fitted dynamic model (for the Ricker model the slope at X_e is $1 - \beta$, which is estimated to be less than -1, both when $X_{-9} = X_e$ and when X_{-9} is free; for the logistic model the slope is $1 - 4\alpha/X_e$, which again is estimated to be less than -1 in both cases). Because of this irregularity in the likelihood function, confidence intervals for the model parameters could not be obtained. Point estimates are given in Table 3.

The values of R^2 are again quite high although not as good as for redfish. While the estmates from the two logistic models are quite compatible with one another, they exhibit some discrepancy with those from the Ricker model. The Ricker model estimates should not be taken too seriously because of the inadequate fit of the model, in spite of the higher R^2 value obtained. Since in the logistic case the fitted model is unstable, there seems little reason to assume that before fishing started the population would be in equilibrium (i.e. $X_{-9} = X_e$). A precise test of this is not possible because of the irregularity of the likelihood surfaces. Thus we will adopt as the best fit the logistic model with X_{-9} free and estimate the MSY at 30 600 t and the catchability at 0.068 per thousand days.

To see how these results compare with other methods, the Gulland and Fox methods were tried on the data as were the Schaefer (1954) and Ricker (1958) surplus production function models. In no case did any of these methods work, the signs of the estimates being incorrect. For the surplus production function models, this was both with q assumed known and q assumed unknown. Sissenwine (1974) estimated catchability q as 0.168 per thousand days, but Deriso (1980) estimated it as 0.018 per thousand days. The estimate obtained above lies in between these two estimates.

Catch Predictions

Estimates of model parameters for redfish were made using only the data for years 1955–71. The data for years 1972–76 was reserved for comparing with predictions from the fitted model following the practice of Huang and Redlack (1981).

In the model of this paper the catch for a given level of effort is a random variable with mean $qE_tX_t + \sigma^2$ and variance $4\sigma^2(qE_tX_t + \sigma^2)$ (see (4)). Given data up to year t and the effort E_{t+1} in year $t + 1$, the ML estimate of the expected catch in year $t + 1$ is

$$(20) \quad \hat{\mathscr{E}}(C_{t+1}) = \hat{q}E_{t+1}\hat{X}_{t+1} + \hat{\sigma}^2$$

where $\hat{q}$, $\hat{\sigma}^2$, and $\hat{X}_{t+1}$ are ML estimates using the data up to year t. Because of the nonlinearity of the problem, calculation of the standard error of this estimate is difficult even when approximate standard errors of the estimates of the model parameters are available. The ML estimate of the standard deviation of the catch in year $t + 1$ is given by

$$(21) \quad 2\hat{\sigma}[\hat{q}E_{t+1}\hat{X}_{t+1} + \hat{\sigma}^2]^{1/2}.$$

Again, calculation of the standard error of this estimate is difficult.

For each of the three models deemed to provide an acceptable fit to the 1955–71 data in the Results section (Ricker with $X_1 = X_e$, and X_1 free, logistic with X_1 free), estimates of the mean and standard deviation of the catch in year $t + 1$, given the effort in year $t + 1$, and catch–effort data up until year t, are presented in Table 4. A graphical representation is given in Fig. 4.

Note that because the results here are *estimates* of the expected value and standard deviation of the upcoming catch, one should not necessarily expect that the observed catch would lie within plus or minus two estimated standard deviations of the estimated mean catch with probability of about 0.95. Because of the sampling error of the estimates the probability of such an event would be considerably less than 0.95.

Taking this fact into account makes the predictions for the years 1974 and 1975 look better than they do at first sight. For example, in the year 1974, for all models, the observed catch is more than four estimated standard deviations from the estimated expected catch. However, the standard error in the estimated expected catch could easily be as large as 4000 or 5000 t (see standard errors of the estimates of MSY, X_1, and X_e in Table 1). If this were the case the total variance (sampling error plus system randomness) of the difference between estimated expected catch and actual catch could be as high as 36 square units. The observed differences would be (just) compatible with this.

It should be noted that the years 1974 and 1975, for which the catch predictions are worst, have effort levels considerably higher than most other years in the data set.

To compare the predictive power of various models, Huang

TABLE 4. One-step-ahead estimates of the mean and standard deviation (in parentheses) of the upcoming catch for each of the years 1972–75 for redfish. Units of catch are thousands of metric tons and units of effort are thousands of hours.

			Estimated expected catch			Estimated expected catch using q modification discussed in text:
			Ricker model			
Year	Effort	Observed catch	X_1 free	$X_1 = X_e$	Logistic X_1 free	Ricker $X_1 = X_e$
1972	38.35	26.04	27.03(2.71)	26.56(2.80)	24.90(2.40)	23.35
1973	30.01	18.37	24.06(2.49)	23.59(2.56)	22.86(2.22)	18.12
1974	44.95	22.16	36.05(3.20)	35.43(3.26)	36.53(2.89)	26.24
1975	55.72	28.25	41.78(4.47)	33.19(3.72)	37.22(3.74)	29.44
1976	39.15	19.97	21.37(2.65)	21.37(3.00)	15.37(2.41)	18.61

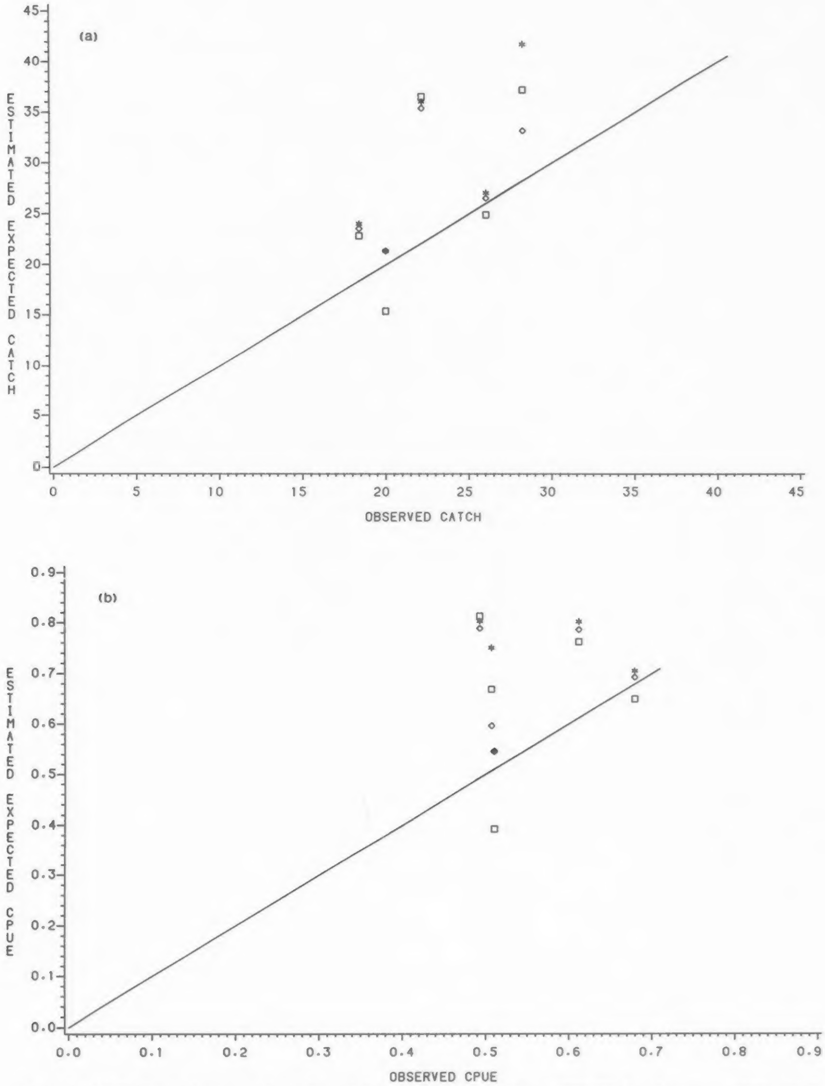

FIG. 4. (a) Estimated expected catch and (b) catch per unit effort (CPUE) for the years 1972–76 for redfish. Dynamic models used are Ricker with X_1 free (∗), Ricker with $X_1 = X_e$ (◇), and logistic with X_1 free (□). Units of catch are thousands of metric tons and units of CPUE are thousands of metric tons per thousand hours.

TABLE 5. Maximum likelihood estimates of model parameters for redfish using a logistic spawner–recruit relation and a lag corresponding to "knife-edge" recruitment at age 2. Units as in Table 1. Data for years 1955–71 were used for "$n = 17$" and data for years 1955–76 used for "$n = 22$".

	$n = 17$		$n = 22$	
	(ii) $X_0 = X_1$	(iii) X_0, X_1 free	(ii) $X_0 = X_1$	(iii) X_0, X_1 free
$\hat{X}_e$	81.32	81.70	79.74	79.23
$\widehat{\mathrm{MSY}}$	25.83	25.76	25.72	25.72
$\hat{\ell}$	0.999	0.998	1.00	1.00
$\hat{q}$	0.0105	0.0105	0.0108	0.0108
$\hat{\sigma}^2$	0.0616	0.0630	0.0741	0.0739
R^2	99.3	99.3	98.9	98.9

TABLE 6. One-step-ahead estimates of the mean and standard deviation (in parentheses) of the upcoming catch for each of five years 1972–75 for redfish using the logistic spawner–recruit model and "knife-edge" recruitment at age 2. Units for catch are thousands of metric tons and units of effort are thousands of hours.

			Estimated expected catch	
Year	Effort	Observed catch	(ii) $X_0 = X_1$	(iii) X_0, X_1 free
1972	38.35	26.04	20.56(2.25)	20.53(2.27)
1973	30.01	18.37	19.34(2.23)	20.38(2.30)
1974	44.95	22.16	32.05(2.84)	33.59(2.83)
1975	55.72	28.25	31.12(3.40)	33.97(3.21)
1976	39.15	19.97	19.72(2.65)	18.82(2.39)

and Redlack (1981) used the measure

$$(22)\quad H = \sum_{t=18}^{22} \left(\frac{C_t}{E_t} - \frac{\hat{C}_t}{E_t}\right)^2$$

where $\hat{C}_t$ is a prediction of C_t. Using (20) as predictor the Ricker model had values of H of 0.192 for X_1 free and 0.127 for $X_1 = X_e$. The logistic model with X_1 free had a value of H of 0.165. Interestingly enough the logistic model with $X_1 = X_e$, which was discarded in the Results section because of an unsatisfactory residual plot, had a value of H of 0.090.

All of these results are considerably worse than the best of the predictions obtained by Huang and Redlack. For example, the best predictions using the Schaefer model had a value of H of 0.044 (when $q = 0.014$) and the best predictions using the Gulland model had a value of H of 0.014 (averaging over 7 yr of effort). However, to obtain these results, Huang and Redlack made the ad hoc adjustment mentioned earlier of inflating the CPUE by a factor 1.5 for the years 1959–64. Without this adjustment neither method worked.

To see how such an adjustment would affect the predictions of the model of this paper, the model was fitted assuming a catchability equal to 2/3 of q for the years 1956–64. This improved the predictive power remarkably. For example, with the Ricker model with $X_1 = X_e$, the predictions of mean catch for the years 1972–75 are given in Table 4. The corresponding value of H was 0.015. This demonstrates that the current model can do at least as well predictively as the Gulland and Schaefer models provided they operate under the same rules with respect to data massaging.

As Huang and Redlack correctly observed, the years 1960–64 are somewhat anomalous. In all the models fitted here, these years produced negative residuals. Furthermore, they represent the first years of a regime of greatly increased fishing effort.

The Dynamic Model

The dynamic model (6), $X_{t+1} = F(S_t; \boldsymbol{\theta})$, was chosen for its simplicity. There is no reason why a more complex dynamic model reflecting particular knowledge of the fishery in question should not be used. For example if there is a time lag in recruitment this can be incorporated into a delay difference equation model of the form

$$(23)\quad X_{t+1} = \ell S_t + F(S_{t-a+1}; \boldsymbol{\theta})$$

where ℓ is a natural survival parameter, a is the age of recruitment (assuming "knife-edge" recruitment), and F is a spawner–recruit relation.

For the two fish stocks considered in this paper, knowledge of the age of recruitment appears to be vague. Most likely there is "continuous" recruitment taking place. However, to see if the use of a delay model can improve the fit, model (23) was fitted to the redfish data using $a = 2$ and 3 and using a Ricker and logistic form for F.

It turned out that the logistic model provided a better fit than the Ricker with $a = 2$ and that neither provided satisfactory fits for $a = 3$, with the maximization routine frequently failing to converge.

When one allows for a delay in the dynamic model, additional starting values must be specified to generate the sequence of X_t values. This was taken into account in fitting the models. With $a = 2$, three cases were considered: (i) $X_0 = X_1 = X_e$, (ii) $X_0 = X_1 =$ a free parameter, and (iii) X_0 and X_1 both free parameters. Taking into account the two parameters of the logistic function F and the survival parameter ℓ, there were thus respectively three, four, and five parameters in the concentrated likelihood (11) in cases (i), (ii), and (iii), respectively.

As before, the model was fitted first using the first 17 yr of catch–effort data (1955–71) and then one-step-ahead catch predictions were made for the years 1972–76. Only results for the logistic model are reported here, since it provided a better fit than the Ricker model.

Table 5 gives parameter estimates for cases (ii) and (iii), both (a) using only the first 17 yr of data and (b) using all 22 yr of data. The case (i) model with starting values X_0 and X_1 both set to X_e did not provide a satisfactory fit. For both models (ii) and (iii), residual plots were satisfactory. It can be seen that the

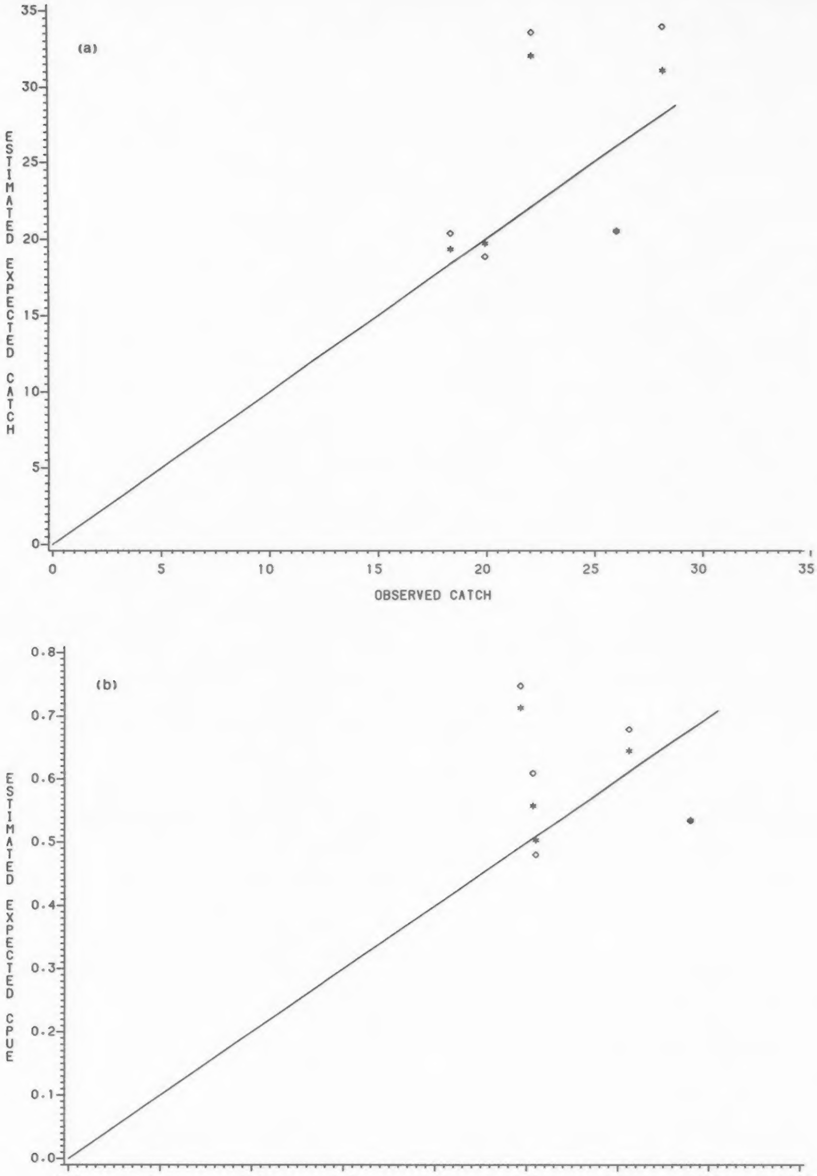

FIG. 5. (a) Estimated expected catch and (b) catch per unit effort (CPUE) for redfish. The dynamic model assumed knife-edge recruitment at the age 2 and is of the logistic form either with $X_1 = X_0$ (∗) or with X_1 and X_0 both free parameters (◇). Units of catch are thousands of metric tons and units of CPUE are thousands of metric tons per thousand hours.

estimates in the two cases are very similar and do not change greatly with the inclusion of the last 5 yr of data. The R^2 values are extremely high, indicating good explanatory power in the model. However, the fact that the survival parameter ℓ is estimated as being effectively 1 leads one to some skepticism as to the veracity of the model. In both cases the irregularity of the log-likelihood prevented the use of asymptotic maximum likelihood theory in obtaining confidence intervals. One-step-ahead estimates of the mean catch and the standard deviation of the catch for the years 1972–76 are given in Table 6. Standard errors for these estimates have not been obtained and the comments in the preceding section on the consequences of this are equally relevant here. Figures 5a and 5b show predictions of catch and CPUE. The predictions are on the whole satisfactory except for the year 1974 where the estimates are on the high side. The values of the index H (defined in (22), preceding section) are (ii) $H = 0.73$ and (iii) $H = 0.101$. It appears that the model incorporating the delay not only provides a better fit to the 1955–71 data than does the model without delay, but also has better predictive power for the years 1972–76. In view of this fact it seems appropriate to revise downwards the estimate of MSY obtained in the Results section to somewhere in the range of 25 000 t.

Stochastic Dynamics

The assumption of deterministic population dynamics is ultimately as unrealistic as the assumption of a deterministic catch production function present in surplus production models. The main thrust of this paper has been to investigate the possibilities for analysis of putting all of the randomness into the catching process and ignoring that in the population dynamics. As shown in previous sections, this approach provides very plausible results. However, is it possible to obtain a synthesis of the two approaches: namely a model that allows explicitly for randomness in both the catching process and in the population dynamics?

To this end, suppose we replace the deterministic dynamic model (6) by a stochastic model of the form

(24) $X_{t+1}|S_t = G(S_t, \epsilon_t; \boldsymbol{\theta})$

where now $\{X_t\}$ and $\{S_t\}$ are sequences of random variables and $\{\epsilon_t\}$ is a sequence of random variables representing environmentally induced fluctuation. For example we could have

(25) $X_{t+1}|S_t = F(S_t; \boldsymbol{\theta}) + \epsilon_t$

where the ϵ_t are independent $N(0, \tau^2)$ random variables and F is a deterministic function or

(26) $X_{t+1}|S_t = \epsilon_t \cdot F(S_t, \boldsymbol{\theta})$

where the ϵ_t are log-normal random variables. In this case the likelihood will involve the randomness in the $\{X_t\}$ process as well as in the catch process. It will be of the form

$$L = \int \text{pr}(\boldsymbol{C}|\boldsymbol{X})\ \text{pr}(\boldsymbol{X})d\boldsymbol{X}$$

where $\boldsymbol{C}$ and $\boldsymbol{X}$ are vectors representing the complete set of C_t and X_t values. While the first term, $\text{pr}(\boldsymbol{C}|\boldsymbol{X})$, can easily be evaluated (it is the same as the likelihood (5) in the case when the X_t are deterministic), the unconditional probability, $\text{pr}(\boldsymbol{X})$, cannot so easily be evaluated. This is because in the $\{X_t\}$ process, as defined in general by (24) (or in particular cases by (25) or (26)), the new state X_{t+1} depends on both (the old state) X_t *and* (the catch) C_t. Thus, while it is straightforward to evaluate the conditional probability $\text{pr}(\boldsymbol{X}|\boldsymbol{C})$, this is not the case for evaluation of the unconditional probability $\text{pr}(\boldsymbol{X})$. This difficulty in expressing the likelihood in a computable form militates against the use of the method of maximum likelihood.

Discussion

Reversing the implicit assumptions made in most conventional methods of analyzing catch–effort data has led to a new method of analysis of such data. This new method is based on the assumption that randomness occurs in the catching process but not in the population dynamics. The new procedure relies on the method of maximum likelihood for parameter estimation, and involves numerical maximization. Provided the likelihood function is smooth, approximate standard errors for model parameters and for MSY can be obtained. Furthermore, approximate confidence intervals can be obtained using the maximum likelihood ratio test procedure.

The idea of using a stochastic catch model for catch–effort data is not entirely new. Allen (1966) minimized the sum of squares between observed catch and expectd catch in order to estimate catchability and population size. However, he used a linear dynamic model and so the method is not applicable for determining MSY, etc. The International Whaling Commission (IWC) has used similar methods: Cooke (1983) and de la Mare and Cooke (1983) both used the root-normal model following Kirkwood (1981) who pointed out that it could be used as an approximation to the Poisson model. However, the thrust of the IWC work is the esitmation of catchability, population abundance, and other vital parameters of whale populations. In contrast, the main thrust of the current paper is in estimating MSY and developing a procedure for making catch predictions. Since the IWC papers all use linear (or no) interperiod dynamic models, the idea of determining MSY does not occur.

In the method described, considerable flexibility is possible in the specification of a deterministic dynamic model. Thus, particular knowledge of the dynamics of a given fishery can be incorporated into this component of the overall model. The essential point is that the model fit the data as assessed by examination of the residuals, the value of the coefficient of determination, R^2, etc. Good predictive power in the model is also desirable. This can be assessed by splitting the data into two parts, chronologically, fitting the model to the first part and then obtaining catch predictions for the latter years. Considerable "trial-and-error" effort may be necessary to find a satisfactory model and there may well be several models which all fit the data. This is all to the good insofar as by comparing the prescriptions of the various models (especially the MSY) one can obtain some idea as to the robustness of the conclusions.

Extensions to the catch model may be possible but have not been examined here. For example, catch models that allow for gear saturation and congestion (Clark 1976, p. 235–240) may be useful. However, in extending the model, care must be taken to avoid an undue proliferation of parameters. Experience in many areas of statistics has shown that, with respect to parameters, parsimony is often the best policy, and that it is usually wisest to use the simplest model that will do the job (see e.g. Ludwig and Walters 1985). With the simplest form of the model used in this paper, four parameters are needed. Often more may be required. With only short time series of reliable data often available, there may be considerable dangers of "over-fitting the model" when further parameters are introduced.

The results obtained on the two sample data sets examined indicate that the method performs better than the Schaefer (1954) and the Gulland (1961) methods. Of course this may not be the case for other data sets and further performance trials of the method are needed.

The method is computationally more complex than the Gulland and Schaefer methods but computation time is not large on a main-frame computer.

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Appendix 1: A Stochastic Model for the Fishing Process

We shall think of a fish stock as comprising a number of catch units. Such units might be individual fish or perhaps more realistically groups or schools of fish. Suppose initially at the start of the fishing season there are X such units in the fish stock and suppose that fishing activity during the season comprises successive soaks of the fishing gear of lengths $t_1, t_2, \ldots, t_k$.

Assume that for a single unit in a given soak

$$\text{pr(unit caught in } (t, t+\Delta) \,|\, \text{not caught before } t) = q\Delta + o(\Delta)$$

where q is a constant reflecting the effectiveness of the gear (the catchability coefficient). It then follows that

$$\text{pr(unit not caught in } (0, t)) = \lim_{\Delta \to 0} (1 - q\Delta + o(\Delta))^{t/\Delta} = e^{-qt}$$

and thence that

$$\text{pr(unit not caught in fishing season)} = \prod_{j=1}^{k} e^{-qt_j} = e^{-qE}$$

where $E = \sum_1^k t_j$ is the total fishing effort during the season and

$$\text{pr(unit caught in fishing season)} = 1 - e^{-qE}.$$

Assuming further that the captures of distinct units constitute independent events, then it follows that the number of units caught, C, in a given season is a binomial random variable with index X and parameter $1 - e^{-qE}$, i.e.

$$C \sim \text{binomial } (X, (1 - e^{-qE})).$$

If the probability $1 - e^{-qE}$ of a given unit being caught is small then the above binomial distribution is well approximated by a Poisson distribution with mean $\lambda = X(1 - e^{-qE})$. Now, $1 - e^{-qE}$ will be small only if qE is small in which case $1 - e^{-qE}$ can be approximated by qE. Thus, if the probability of an individual unit being caught is small, the distribution of C can be approximated by a Poisson distribution with mean qEX, i.e. C will have probability mass function

$$f(C) = \frac{e^{-qEX}\,(qEX)^C}{C!} \qquad C = 0, 1, 2, \ldots$$

Note that C and X are measured in numbers of units. Also, $E(C) = \text{var}(C) = qEX$.

Now suppose each catch unit has biomass m and that C_B and X_B represent catch and initial stock size in biomass units. Then we have

$$\frac{C_B}{m} \sim \text{Poisson}\left(\frac{qEX_B}{m}\right).$$

It follows that

$$E(C_B) = mE(C) = m \cdot \frac{qEX_B}{m} = qEX_B$$

and

$$\text{var}(C_B) = m^2\,\text{var}(C) = m^2\,\frac{qEX_B}{m} = m \cdot qEX_B.$$

Thus, in biomass units the variance of catch is proportional to (but in general, not equal to) the expected catch.

An alternative model which is more convenient than the above and which provides a good approximation to it is

$$\sqrt{C_B} \sim N(\sqrt{qEX_B}, \sigma^2).$$

It is easy to show that for this model that

$$E(C_B) = qEX_B + \sigma^2$$

and

$$\mathrm{var}(C_B) = 4\sigma^2(qEX_B + \sigma^2).$$

Thus, this root-normal model shares the property with the above Poisson model that

$$\mathrm{var}(C_B) \propto E(C_B).$$

Note that the above model for the fishing process is highly simplified. It can be criticized on many grounds; the assumptions of equal sized catch units, of independence of captures of units, and of the probability of capture being small are all of questionable validity. We do not here offer it in a reductionistic sense as being the justification for the employment of the root-normal model. Rather we offer as justification of the root-normal model the fact that it seems to fit the observed data rather well. The above model of the fishing process we can regard as an interestng fiction which contains some elements of truth.

Appendix 2: Use of the Maximum Likelihood Ratio Test Procedure for Obtaining Confidence Intervals for Model Parameters

The method (see Cox and Hinkley 1974, p. 322) is based on the fact that for testing H_0: $\theta = \theta_0$ vs. H_1: $\theta \neq \theta_0$, with nuisance parameters present, asymptotically the statistic

$$\text{(A2.1)} \quad W = -2 \ln \Lambda$$

has a χ^2_1 distribution under H_0, where Λ is the maximum likelihood ratio statistic:

$$\text{(A2.2)} \quad \Lambda = \frac{\max\limits_{\Omega_0} L(\boldsymbol{\theta}; \boldsymbol{X})}{\max\limits_{\Omega} L(\boldsymbol{\theta}; \boldsymbol{X})}$$

where Ω is the parameter space and Ω_0 is the subset of Ω for which $\theta = \theta_0$.

Suppose that the dynamic model (6) has k parameters, i.e. $\boldsymbol{\theta} = (\theta_1, \ldots, \theta_k)$. Depending on whether X_1 is considered a free parameter, or whether X_1 is set equal to X_e, there will be k or $k + 1$ parameters in the concentrated likelihood (11). For the sake of illustration, consider the case with X_1 free, and consider the problem of estimating the parameter θ_1. A $100(1 - \alpha)\%$ confidence interval for θ_1 is given by the set of null values of θ_1 which would not be rejected at the level α using the maximum likelihood ratio test. From the asymptotic distribution of W, it follows that an approximate $100(1 - \alpha)\%$ confidence interval for θ_1 is given by

$$\text{(A2.3)} \quad \{\theta_1 \colon \hat{\ell}(\theta_1, \tilde{\theta}_2, \ldots, \tilde{\theta}_k, \tilde{X}_1) \geq \ell(\hat{\theta}_1, \hat{\theta}_2, \ldots, \hat{\theta}_k, \hat{X}_1) - \frac{1}{2}\chi^2_{1,\alpha}\}$$

where $\hat{\ell}$ is the concentrated likelihood given by (11); $\hat{\theta}_1, \hat{\theta}_2, \ldots, \hat{\theta}_k, \hat{X}_1$ are the ML estimates of $\theta_1, \theta_2, \ldots, \theta_k, X_1$; $\tilde{\theta}_2, \ldots, \tilde{\theta}_k, \tilde{X}_1$ are the ML estimates of $\theta_1, \ldots, \theta_k, X_1$ when θ_1 is fixed at a given value; and $\chi^2_{1,\alpha}$ is the $100\alpha\%$ percentage point of the χ^2_1 distribution.

Computationally this procedure is fairly lengthy, because it involves choosing a grid of values of θ_1, and for each obtaining the ML estimates $\theta_1, \ldots, \tilde{\theta}_k, X_1$ of the other parameters. The function $\hat{\ell}(\theta_1, \tilde{\theta}_2, \ldots, \tilde{\theta}_k, \tilde{X}_1)$ can then be plotted against θ_1, and the set of values of θ_1 satisfying (A2.3) can be found graphically.

A similar procedure can be used for obtaining confidence intervals for the other model parameters. It should be noted that the method is not appropriate in the cases where the likelihood surface is very irregular. The advantage of the method is that it is invariant under transformations of the parameters. Thus if there is a parameter transformation which makes the likelihood surface close to a quadratic, then the above procedure will provide accurate confidence intervals.

Appendix 3: Asymptotic Variance of the MSY Estimate for the Ricker Model

For the Ricker model

$$\text{(A3.1)} \quad X_{t+1} = S_t \exp\{\beta(1 - S_t/\alpha)\}$$

the MSY is given by

$$\text{(A3.2)} \quad S_0 \exp\{\beta(1 - S_0/\alpha)\} - S_0$$

where S_0 is the solution to

$$\text{(A3.3)} \quad \frac{d}{dS}[S \exp\{(1 - S/\alpha)\}] = 1$$

i.e. $(1 - (\beta/\alpha)S) \exp\{\beta(1 - S/\alpha)\} = 1$. Denote the MSY by $M(\alpha,\beta)$. From the invariance property of ML estimates it follows that the ML estimate of the MSY is $\hat{M} = M(\hat{\alpha},\hat{\beta})$ where $\hat{\alpha}$ and $\hat{\beta}$ are ML estimates of α and β.

Furthermore, the asymptotic variance of $\hat{M}$ is equal to $\boldsymbol{d}' I_0^{-1} \boldsymbol{d}$ where

$$\boldsymbol{d}' = \left(\left.\frac{\partial M}{\partial \alpha}\right|_{\hat{\alpha},\hat{\beta}}, \left.\frac{\partial M}{\partial \beta}\right|_{\hat{\alpha},\hat{\beta}}\right)$$

and $\hat{I}_0^{-1}$ is the 2×2 part of the inverse of the observed information matrix corresponding to the parameters α and β (Cox and Hinkley 1974).

To obtain the derivatives in the vector $\boldsymbol{d}'$ we first note that from (A3.2) and (A3.3), M can be expressed as

$$\text{(A3.4)} \quad M(\alpha,\beta) = \frac{\beta S_0^2}{\alpha - \beta S_0}.$$

From this we find the derivatives $\partial M/\partial\alpha$ and $\partial M/\partial\beta$, which of course depend on the derivatives $\partial S_0/\partial\alpha$ and $\partial S_0/\partial\beta$. These latter derivatives can be obtained from (A2.3) by implicit differentiation. After some algebra we get

$$\frac{\partial M}{\partial \alpha} = \frac{\beta}{\alpha} \cdot \frac{S_0^2}{\alpha - \beta S_0}$$

and

$$\frac{\partial M}{\partial \beta} = \frac{S_0(\alpha - S_0)}{\alpha - \beta S_0}.$$

Substituting ML estimates $\hat{S}_0$, $\hat{\alpha}$, and $\hat{\beta}$ in the above expressions yields the vector $\boldsymbol{d}'$. Furthermore, $\hat{I}_0^{-1}$ can be found from the numerically determined second derivatives of the log-likelihood at its maximum. Thus, a numerical value of the asymptotic variance of $\hat{M}$ can be determined.

Growth Decline in Subyearling Brook Trout (*Salvelinus fontinalis*) after Emergence of Rainbow Trout (*Salmo gairdneri*)

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Rose, G. A. 1986. Growth decline in subyearling brook trout (*Salvelinus fontinalis*) after emergence of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 43: 187–193.

In a tributary of Lake Superior, brook trout (*Salvelinus fontinalis*) subyearlings, after emergence in April, initially gained length at 0.51 mm/d and weight at a specific growth rate per day (*G*) of 0.058. After the emergence of larval rainbow trout (*Salmo gairdneri*) in June, however, length increments of brook trout declined to 0.05 mm/d and *G* was reduced to 0.005. During August, brook trout growth rebounded somewhat (0.12 mm/d; $G = 0.008$). Rainbow trout subyearlings, by contrast, grew at relatively constant rates of 0.42 mm/d and *G* of 0.040, from emergence until September. By late August, mean weights of brook and rainbow trout, 2026 and 2282 mg, respectively, did not differ significantly. Stream positions occupied by brook trout, characterized by flows of less than 20 cm/s and depths of less than 40 cm, did not change over the first summer. During June and July, stream positions of rainbow trout subyearlings coincided with those of brook trout. During August, however, rainbow trout moved to faster waters (>20 cm/s). The taxonomic composition of the diets of the two species did not differ. Mean width of food items consumed was linearly correlated with the total length of the fish ($r = 0.97$). The range of sizes of items eaten by the two species overlapped considerably by mid-June. For brook trout, mean food size increased, and amount consumed decreased, after the emergence of rainbow trout larvae. Growth reduction during the first summer, an outcome of interspecific competition for food and space, may result in increased overwintering mortality of fish at high latitudes, and be a mechanism by which brook trout are excluded by rainbow trout.

Dans un tributaire du lac Supérieur, des ombles de fontaine (*Salvelinus fontinalis*) de moins de un an ont, après leur éclosion en avril, crû d'abord à un taux de 0,51 mm/jour et augmenté de poids à un taux de croissance spécifique par jour (*G*) de 0,058. Cependant, après l'apparition des larves de truite arc-en-ciel (*Salmo gairdneri*) en juin, l'augmentation de longueur des ombles de fontaine est tombée à 0,05 mm/jour et *G* a diminué jusqu'à 0,005. En août, la croissance des ombles de fontaine s'est élevée quelque peu (0,12 mm/jour; $G = 0{,}008$). Par contre, les truites arc-en-ciel de moins de un an se sont développées à des taux relativement constants de 0,42 mm/jour et de 0,040 (*G*), de leur éclosion jusqu'en septembre. À la fin d'août, le poids moyen des ombles de fontaine et des truites arc-en-ciel, respectivement de 2026 et de 2282 mg, ne différait pas sensiblement. Les emplacements occupés par les ombles de fontaine dans le cours d'eau, caractérisés par des débits inférieurs à 20 cm/s et des profondeurs ne dépassant pas 40 cm, n'ont pas changé au cours du premier été. En juin et en juillet, les emplacements occupés par les truites arc-en-ciel de moins de un an dans le cours d'eau coïncidaient avec ceux des ombles de fontaine. Cependant, en août, les truites arc-en-ciel se sont rendues dans des eaux plus rapides (>20 cm/s). La composition taxonomique des proies ingérées par les deux espèces ne différait pas. Il y avait une corrélation linéaire entre la largeur moyenne des proies ingérées et la longueur totale des poissons ($r = 0{,}97$). À la mi-juin, les échelles de taille des proies consommées par les deux espèces se chevauchaient considérablement. Pour l'omble de fontaine, la taille moyenne des proies a augmenté et la quantité ingurgitée a diminué après la sortie des larves de truites arc-en-ciel. La réduction de la croissance au cours du premier été, résultat de la concurrence interspécifique pour l'espace et la nourriture, peut entraîner une mortalité plus importante des poissons pendant l'hiver à des latitudes élevées et constituer un mécanisme par lequel les ombles de fontaine sont écartés par les truites arc-en-ciel.

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The introduction of exotics has often led to displacement or elimination of indigenous species with similar niches (Kelly et al. 1980; Li and Moyle 1981). Competitive advantages, thought to be responsible for such exclusions, are seldom fixed or constant, but vary with season, developmental stage, and environmental fluctuations (Spiller 1984a; Abrams 1980; Chesson and Warner 1981). Thus, critical periods may exist when competition between given species is intense and reduction mechanisms functional. Studies conducted at other times or on other developmental stages may fail to detect any interaction, or even show reverse dominance (Spiller 1984b).

Brook trout (*Salvelinus fontinalis*) have lost ground since the introduction of rainbow trout (*Salmo gairdneri*) to eastern North America in the 1800s (Power 1980). Often, after the two species have become sympatric, the brook trout has been virtually eliminated (King 1937, 1942; Kelly et al. 1980; Larson and Moore 1985). Although competition has been routinely invoked as a cause of the exclusion of brook trout (King 1937, 1942; Balon 1980; Power 1980; Waters 1983; Larson and

Moore 1985), a competitive mechanism capable of causing exclusion has not been demonstrated.

For brook and rainbow trout, spatial overlap in habitat is likely maximal during the first summer. Recently emerged rainbow trout occupy a wide range of microhabitats, including shallow waters at stream margins and riffles (Hartman 1965). During their first year, they move to habitats with faster waters and coarser substrates (Everest and Chapman 1972). In contrast, brook trout utilize slower waters throughout their lives (Gibson 1973; Cunjak and Green 1984). Subyearling brook trout feed on stream drift (Lord 1933; Griffith 1974) as do subyearling rainbow trout (Jenkins et al. 1970; Johnson and Ringler 1980).

Competition may alter growth rates. Removal of a competitor may increase growth in remaining species (Gibson and Dickson 1984; Moore et al. 1983); addition of a competitor may decrease growth in species already present (Hanson and Leggett 1985). Poor growth during the first summer of life has been correlated with elevated overwintering mortality of fish at high latitudes (Toneys and Coble 1979, 1980; Oliver and Holeton 1979; Hunt 1969). Thus, competitive effects on growth during early life could regulate adult abundance (Gutreuter and Anderson 1985), and cause exclusion of species.

I hypothesized that a critical period of competition would occur during the first months of coexistence, and that during this period the growth rate of brook trout would be depressed, thus reducing their survivorship through the first winter.

Study Site

This hypothesis was tested in a tributary of Lake Superior, the Goulais River, located 30 km north of Sault Ste. Marie, Ontario. Rainbow trout were originally stocked in eastern Lake Superior in 1895 (MacKay 1963). Stocking of rainbow trout in the Goulais River has occurred during the past 20 yr (O. Wohlgemuth, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont., pers. comm.). Anecdotal evidence suggests that brook trout were abundant in the Goulais prior to the introduction of rainbow trout. Recent studies have shown that rainbow trout are now substantially more abundant in all parts of the river accessible to them, and that brook trout are rare in most of that area (Ontario Ministry of Natural Resources, Sault Ste. Marie District, unpubl. data). Brook trout larvae were found to be abundant, however, at a site in the Goulais about 80 km from Lake Superior. This was also a spawning site for rainbow trout.

The study site was 500 m in length; river width ranged from 36 to 88 m, but was 50% emergent gravel bars at its widest point. Major substrates were gravel, rubble, cobble, and angular rock. Secondary channels and backwaters occur on each side of the river and between the extensive gravel bars. Overhanging vegetation and fallen trees shaded approximately 30% of the banks; the remainder were bare gravel−cobble bars. Water depth and velocities varied seasonally and in response to rainfall. During June approximately 50% of the area was less than 60 cm deep and had flows of less than 20 cm/s (deepest zones were 200 cm, fastest water was 100 cm/s). Water quality characteristics in June were pH 7.1, alkalinity 9.2 mg/L, oxygen 9.3 mg/L, color nil, and clarity to substrate at all points. Water temperatures ranged from 4°C in April to 18°C in August, but decreased as much as 5° subsequent to precipitation events.

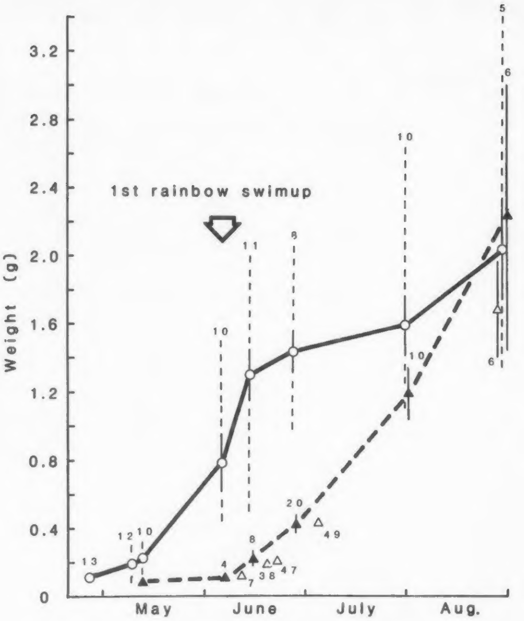

FIG. 1. Growth in weight (mean ± SE) of sympatric brook trout (○) and rainbow trout (▲) and allopatric rainbow trout (△) subyearlings in the Goulais River during 1984. Broken vertical lines are ranges for data of sympatric brook trout. Numbers indicate *n*.

Methods

Sampling was conducted during 1984. Fish were collected by a two- or three-person crew with a Smith-Root 12-V DC backpack electrofisher and hand-held catching nets. All areas with depths of less than 1 m were sampled at the study site and at six other sites on the river. Brook trout subyearlings were present only at the study site; rainbow trout subyearlings were present at all sites. Brook trout subyearlings and yearlings and rainbow trout yearlings were collected from April 28 to August 30. Rainbow trout subyearlings were collected from May 13, at which time they were still in the gravel, until August 30. Densities of subyearlings were calculated from the number of fish electroshocked and the total area sampled. No error term can be assigned to estimates so calculated. Fish were stored in 10% Formalin. Total weight (milligrams) and length (millimetres) were determined for each individual. A correction factor of 1.035 was applied to length data because of shrinkage during storage (Wagner 1975). Changes in weight were assessed by the specific growth rate (G), defined as the change in the natural logarithm of weight per day of the growth interval. Stomach contents were examined and frequency of occurrence and estimates of wet weight (percent by volume of each item × total weight) for each diet item were determined.

Depth of water (centimetres), surface flow (centimetres per second), and substrate type (sand, gravel (0.5−5 cm diameter)), cobble−rubble (>5−20 cm), or boulders (>20 cm) were recorded for each site where a fish was observed.

Statistical comparisons were made with analysis of variance and significance declared if $P < 0.05$, unless otherwise indicated.

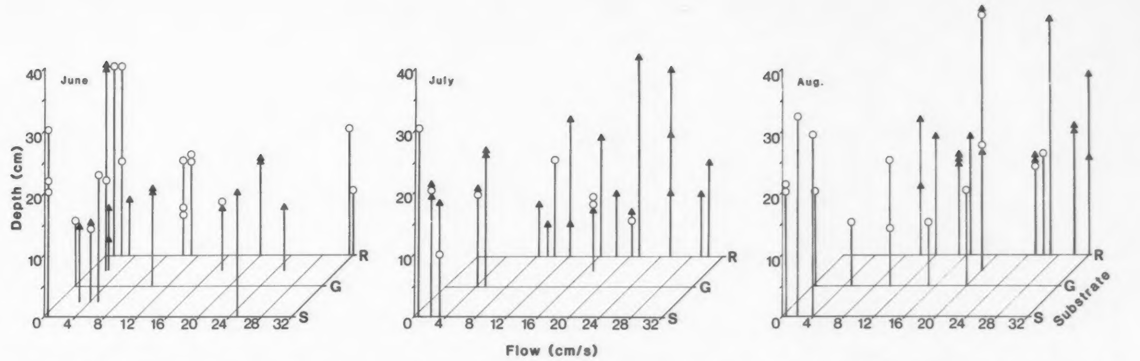

FIG. 2. Depth, surface flow, and substrate (S = sand, G = gravel, R = cobble–rubble) at sites occupied during June, July, and August by subyearling brook trout (○) and rainbow trout (▲).

Results

During April and early May, free swimming brook trout larvae were numerous (density $0.5/m^2$) at the study site. Densities declined to less than $0.3/m^2$ in mid-May after a major flooding event caused by heavy rains. Free-swimming rainbow trout larvae were first observed on June 6, and by mid-June were abundant (density $0.5/m^2$). There was no indication that numbers of brook trout decreased in relation to the emergence of rainbow trout. By late August, the densities of brook and rainbow trout subyearlings were 0.2 and $0.3/m^2$, respectively. At the other sites, densities of allopatric subyearling rainbow trout ranged from 0.1 to $1.2/m^2$ in June and early July. Density declined to $0.4/m^2$ by late August at the site with the highest density in June; no other sites were sampled at that time.

On April 28, brook trout larvae had a mean weight of 80 mg (Fig. 1). Growth was rapid until mid-June, when mean weight was 1304 mg. The value of G over this interval was 0.058 and increments in total length averaged 0.51 mm/d. From late-June until the end of July, however, growth virtually ceased; G declined to 0.005 and mean daily length increments decreased to 0.05 mm. During August, growth rebounded marginally, but G increased only to 0.008 and length gains increased only to 0.12 mm/d.

On June 6 at the study site, rainbow trout larvae had a mean weight of 80 mg (Fig. 1). Growth was uninterrupted and relatively uniform until September. Over this period, G was 0.040 and gains in total length averaged 0.42 mm/d. At the other sites, mean weights of allopatric rainbow trout subyearlings were consistently below the growth curve indicated at the study site.

Brook trout were significantly heavier than rainbow trout until the end of July; by September, however, mean weights, 2026 and 2282 mg, respectively, did not differ significantly. Yearling brook and rainbow trout did not differ significantly in weight; means were 11.2 ($n = 4$) and 11.6 g ($n = 16$), respectively. Sample sizes of yearlings were too small to permit within-year analysis of growth.

During April and May, brook trout subyearlings were observed only in waters having depths of less than 20 cm and surface flows less than 15 cm/s. From June to late August, surface flows and depths of stream positions where brook trout were observed did not change significantly (Fig. 2). During June, July, and August, brook trout occupied positions characterized by mean (±SE) surface flows of 9 ± 3, 9 ± 3, and 11 ± 3 cm/s, respectively, and mean depths of 16 ± 2, 15 ± 3, and 19 ± 2 cm, respectively. Proportions of substrate types for sites occupied by brook trout changed significantly between June and August (chi square = 11.47, df = 2); during June, 69% of positions were over cobble–rubble whereas during August, 73% were over sand or gravel.

The stream positions occupied by rainbow trout during June were in close proximity to those of brook trout; mean (±SE) surface flow and depth of rainbow trout positions were 10 ± 3 cm/s and 14 ± 4 cm, respectively (Fig. 2). During July, some rainbow trout were observed in faster waters (>20 cm/s) with coarser substrates, but surface flows and depths (mean ± SE of 14 ± 2 cm/s and 16 ± 2 cm, respectively) did not differ significantly from those of brook trout. By late August, however, an increased proportion of rainbow trout occupied sites in waters with greater surface flows (mean ± SE of 21 ± 2 cm/s) than sites occupied by brook trout.

Allopatric rainbow trout subyearlings occupied positions during June and July with depth, flow, and substrate characteristics similar to those at the study site. Mean (±SE (n)) depths were 18 ± 1 (69) and 19 ± 1 cm (57), respectively; flows were 6 ± 1 (69) and 15 ± 2 cm/s (57), respectively; substrates were primarily cobble–rubble. By late August, as at the study site, rainbow trout subyearlings occupied positions with higher surface flows (34 ± 5 cm/s (6)), similar depths (20 ± 1 (6)), and coarser substrates (4 of 6 over rubble–boulders) as compared with positions occupied during June and July.

Yearling brook trout were found in deeper (mean ± SE of 36 ± 6 cm), but not faster (mean ± SE of 15 ± 5 cm/s) water than were subyearlings. In each case, yearling positions were associated with overhanging banks. Yearling rainbow trout were found in significantly deeper (mean ± SE of 25 ± 4 cm) and faster (mean ± SE of 30 ± 6 cm/s) water than were subyearlings of either species or yearling brook trout. Yearling rainbow trout occupied positions near the cover of boulders in midstream bed as well as under shaded bank areas.

The taxonomic composition of the diets of the two species differed little; both fed primarily on subadult aquatic dipterans, trichopterans, and ephemeropterans and adult insects of various orders (Table 1). Mean width of food items consumed was linearly related to the total length of the fish, regardless of species ($r = 0.97$, for combined data) (Fig. 3). When rainbow trout larvae emerged, however, the mean size of food items of brook trout temporarily increased above that predicted by the food size-fish size regression (Fig. 4). The range of sizes of

TABLE 1. Stomach contents of subyearling brook trout, before and after the emergence of rainbow trout, and subyearling rainbow trout, in sympatry with brook trout and in allopatry at other sites, from the Goulais River, May to August 1984 (*n* in parentheses; %f = frequency of occurrence, expressed as percentage; %wt = percent of total wet weight; tr = trace).

	Brook trout				Rainbow trout			
	Pre-rainbow (45)		With rainbow (34)		Sympatric (48)		Allopatric (138)	
	%f	%wt	%f	%wt	%f	%wt	%f	%wt
Adult Insecta	42	19	41	22	40	39	3	5
Subadult								
Ephemeroptera	44	33	30	30	20	21	60	51
Tricoptera	39	24	38	14	18	6	10	5
Diptera	42	19	29	10	53	25	62	34
Catostomus spp. and Cyprinid fry			12	16	1	tr	3	5
Collembola	10	4	2	tr	8	2	1	tr
Ostracoda	3	tr			10	2		
Copepoda					1	tr		
Arachnida					12	5		
Hirudinea			1	2				
Amphipoda			8	5	1	tr		
Nematoda					1	tr		
Hydracarina			2	1	1	tr	1	tr
Tardigrada	18	tr						

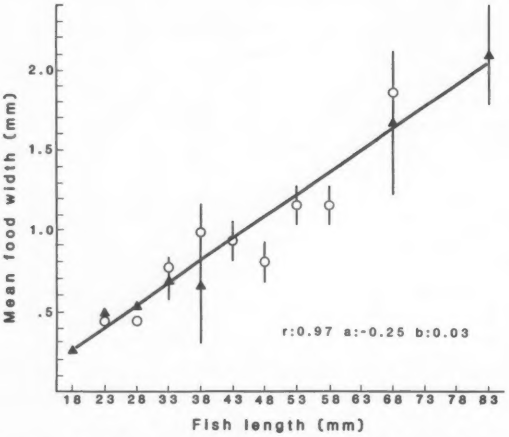

FIG. 3. Width of food items (mean ± SE) found in stomachs of subyearling brook trout (○) and rainbow trout (▲) in relation to total length of fish.

items eaten by the two species overlapped considerably by mid-June, and mean food sizes by late June were not significantly different. The minimum size of food items was the same for both species and did not change during the first summer.

The quantity of food in the stomachs of brook trout, expressed as percent of body weight, declined significantly after the emergence of rainbow trout larvae from 3.1 ($n = 45$) to 1.4 ($n = 19$). During August, the stomach contents of brook trout increased significantly to 5.5% ($n = 15$) of body weight. At the study site, and at the other sites under allopatric conditions, rainbow trout stomach contents were 2.5 ($n = 48$) and 2.2% ($n = 150$) of body weight, respectively, and did not vary significantly among months.

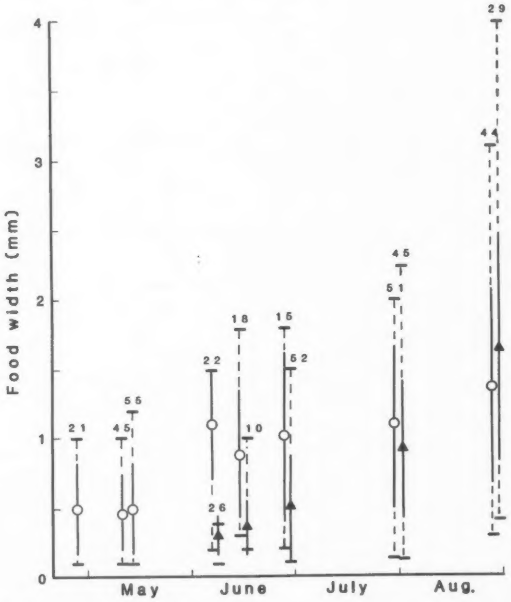

FIG. 4. Width of food items (mean ± SE) found in stomachs of subyearling brook trout (○) and rainbow trout (▲) of specific ages. Broken vertical lines are ranges. Numbers indicate *n*.

Discussion

Prior to the emergence of rainbow trout from the gravel, brook trout growth was typical of the species at this latitude. Subyearling brook trout typically gain length at a rate of 0.45 mm/d over the growth season (Power 1980). Data in Carlander (1969) indicate that specific growth rates (per day) of

0.03−0.04 are typical of subyearling brook trout. In three Michigan rivers, at sites that contained fair to large populations of naturally spawned brook trout, subyearlings increased in length linearly from May until September, illustrating growth ranges thought typical of latitudes similar to our study site (Cooper 1953) (Fig. 5). Cooper attributed growth differences among subyearlings from these three rivers to differences in food availability; temperatures at the three sites were similar to each other and to those in the Goulais River during the present study.

Subsequent to the emergence of rainbow trout, the growth of brook trout declined to well below typical rates. The only available data on growth of subyearling brook and rainbow trout in sympatry in other systems were given by Whitworth and Strange (1983). Using their data, I calculated that average gains in length for brook trout were >0.5 mm/d prior to the emergence of rainbow trout, but decreased to 0.25 mm/d after their emergence. In contrast, rainbow trout grew at >0.7 mm/d (assuming late May emergence at an average size of 25 mm). These calculations should be interpreted with some caution, however, since the fish included in the calculations were from several areas of a river in which productivity may have been unequal and the proportions of the two species varied considerably. Nevertheless, the apparent decline in growth of brook trout after the emergence of rainbow trout is remarkably similar to that found in this study.

Rainbow trout were somewhat smaller at sites where brook trout were absent. Over 80% of the fish included in these data are from sites where densities in June were higher than at the study site. Although productivity was not quantified during the present work and between-site comparison is made with caution, it is possible that the lesser growth reflects intraspecific competition and is density dependent.

Stream space and food are inextricably linked and are competed for by stream salmonids (Chapman 1966; Slaney and Northcote 1974; Fausch and White 1981). Thus, species whose spatial distributions differ are less likely to compete for food. Brook trout have been sympatric with Atlantic salmon (*Salmo salar*) in coastal rivers of eastern North America since at least the last ice age. These species exhibit behavior which minimizes competition (Gibson and Dickson 1984; Gibson and Power 1975). Predictably, growth of subyearling brook trout did not decline after the emergence of salmon 2−3 wk later in two rivers in Nova Scotia (Randall 1982).

By contrast, no spatial segregation of indigenous brook trout and exotic rainbow trout was apparent during June and July. The greater rheophilic abilities of the rainbow trout were not apparent until juveniles reached a length of approximately 40 mm. Prior to their attainment of this size, the potential exists for competition for food or space between these two species. The general field observations of Larson and Moore (1985) that habitat use by subyearlings of these species was very similar supports these conclusions. Cunjak and Green (1983) argued that in Newfoundland streams, subyearling rainbow trout occupied faster water than did subyearling brook trout. However, their argument does not address the critical period of the first 1−2 mo of coexistence, as it is based on a comparison of mean flows at sites occupied by these species between April and October.

Other species of salmonids have been shown to exhibit similar divergences in niche overlap with age. Under controlled laboratory conditions, rainbow trout and coho salmon (*Oncorhynchus kisutch*) subyearlings utilized space, depth, and current in the same manner after emergence of trout larvae, but progressively diverged in utilization patterns during their first year (Hartman 1965).

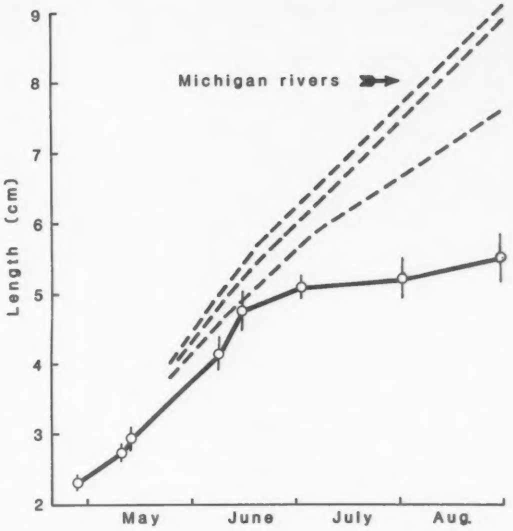

FIG. 5. Growth in length (mean ± SE) of brook trout in the Goulais River during 1984 (○) and in three northern Michigan rivers (data from Cooper 1953).

The decreased growth of brook trout, linked with evidence of dietary and spatial overlap demonstrated in this study, is strong evidence of competition between these species during their first summer. My data suggest that during June and July, when the more abundant rainbow trout cooccurred with brook trout, rainbow trout removed smaller food items in the stream drift which were previously available to the brook trout. Brook trout then fed on remaining items that had sizes nearer the upper range available to them. This restriction of diet resulted in brook trout consuming less food. By late August, when rainbow trout had moved to sites with greater flows, brook trout had greater access to available food, and their stomach contents increased accordingly. In contrast, feeding by rainbow trout did not appear to be affected by the presence of brook trout. Stomach content data reported here are similar to those in the literature (Lord 1933; Jenkins et al. 1970; Johnson 1981).

Behavioral interactions may reduce foraging efficiency (Brown 1945; Stauffer 1977a). Thus, energy and time expenditures by brook trout, in attempts to extirpate rainbow trout larvae from established territories, may have contributed to a decline in the magnitude and metabolic efficiency of feeding. Laboratory observations have indicated that subyearling rainbow trout are more aggressive than subyearling brook trout (unpublished data). Thus, although smaller initially, the more numerous rainbow trout may have been capable of reducing or even preventing feeding by brook trout. These findings call into question the long-held axiom that greater size equals dominance (Newman 1956; Chapman 1966). My work shows that smaller individuals, especially in larger numbers, may attain dominance and eventually larger size.

The low numbers of yearling brook trout encountered during this study point to high levels of winter mortality related to poor first year growth. Applying my data to Hunt's (1969) regression of survival as a function of first summer growth of brook trout in a Wisconsin stream indicates that few Goulais River brook trout would survive their first winter. These findings suggest that at high latitudes, growth reduction during the first summer may be a major determinant of relative population sizes of competiting species.

Brook trout abundance is almost certainly dependent on the relative abundance of potential competitors. Rainbow trout abundance varies widely, for reasons not entirely understood. Beneficial abiotic factors and spawning site requirements may differ between brook trout and rainbow trout (Seegrist and Gard 1972). Where conditions are highly suitable for rainbow trout, brook trout may be eliminated. In five similar tributaries of Lake Superior in Michigan, three rivers with average densities of subyearling rainbow trout of 0.4, 0.6, and 0.8/m^2 sustained extant brook trout populations. Two rivers having average densities of subyearling rainbow trout of 1.8 and 2.6/m^2 contained no brook trout (Stauffer 1977b). Cunjak and Green (1983) found that abundances of brook trout were severalfold less in Newfoundland streams where rainbow trout were present than where they were absent. Larson and Moore (1985) showed that brook and rainbow trout have reciprocal abundances in Appalachian streams. For these similar salmonids, and others such as the brown trout (*Salmo trutta*), a total potential biomass may exist. Interactions such as I have demonstrated, mediated by a myriad of environmental factors, determine the proportion of each species. The difficulty for brook trout appears to be that over much of its native range, sites where it can remain abundant in the presence of rainbow trout are limited.

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Size-Limited Predation, Winterkill, and the Organization of *Umbra–Perca* Fish Assemblages

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Tonn, W. M., and C. A. Paszkowski. 1986. Size-limited predation, winterkill, and the organization of *Umbra–Perca* fish assemblages. Can. J. Fish. Aquat. Sci. 43: 194–202.

We compared population densities and size structures of central mudminnows (*Umbra limi*) occurring with and without yellow perch (*Perca flavescens*) in six small lakes in northern Wisconsin over a 6-yr period. Our observations suggested that a size-dependent predator–prey interaction was a major mechanism organizing these assemblages. Densities of mudminnows cooccurring with perch averaged 12% of populations in mudminnow-only lakes. Large mudminnows (≥76 mm total length) predominated in populations with perch whereas smaller fish predominated in single-species assemblages. Following severe winterkills of adult perch in two lakes, mudminnow densities increased significantly due to high survival and recruitment of yearlings. Increases in small mudminnows lasted only a year: densities and size distributions returned to prewinterkill patterns when perch that had survived winterkill attained lengths >13 cm. To examine the role of size-limited predation, we performed an experiment in 2000-L tanks, varying the initial size distributions of mudminnows and perch and measuring size-specific survival among mudminnows. Predation in the experimental populations was greatest when large perch (121–180 mm) were with populations of predominantly small mudminnows (<76 mm); smaller perch (114–132 mm) were significantly less successful as predators whereas large mudminnows were significantly less vulnerable to predation by even large perch. Despite this interaction, central mudminnows coexist at low densities with yellow perch; possible factors permitting coexistence are fish sizes and spatial and structural refuges.

Nous avons comparé sur une période de 6 ans la densité de population et la structure des tailles chez des umbres de vase (*Umbra limi*), avec et sans la présence de perchaudes (*Perca flavescens*), dans six petits lacs situés dans le nord du Wisconsin. Nos observations nous ont portés à croire qu'une interaction prédateur–proie en fonction de la taille constituait un mécanisme important à l'origine de ces assemblages. La densité des umbres de vase coexistant avec des perchaudes équivalait en moyenne à 12 % des populations rencontrées dans les lacs où se trouvaient uniquement des umbres de vase. Les populations comprenant des perchaudes étaient constituées surtout de gros umbres de vase (longueur totale ≥76 mm), tandis qu'on retrouvait surtout de petits poissons dans les assemblages constitués d'une seule espèce. Suite à la mortalité importante de perchaudes adultes survenue pendant l'hiver dans deux lacs, la densité des umbres de vase a beaucoup augmenté en raison de la survie élevée et du recrutement de poissons d'un an. L'augmentation du nombre de petits umbres de vase ne s'est produite qu'au cours d'une année; la densité et la répartition des tailles sont revenues à ce qu'elles étaient avant la période de mortalité hivernale, au moment où les perchaudes qui avaient survécu atteignaient des longueurs de plus de 13 cm. Pour étudier le rôle joué par la prédation en fonction de la taille, nous avons réalisé une expérience dans des réservoirs de 2 000 L, en modifiant la répartition initiale des tailles des umbres de vase et des perchaudes et en calculant le taux de survie en fonction de la taille parmi les umbres de vase. La prédation dans les populations expérimentales était plus importante lorsque de grosses perchaudes (de 121 à 180 mm) se trouvaient avec des populations constituées surtout de petits umbres de vase (<76 mm); les perchaudes plus petites (de 114 à 132 mm) étaient beaucoup moins efficaces comme prédateurs, et les gros umbres de vase étaient beaucoup moins exposés à la prédation, même de la part des grosses perchaudes. Malgré cette interaction, les umbres de vase coexistent en petits nombres avec les perchaudes; les facteurs possibles qui permettent la coexistence sont la taille des poissons et les barrières spatiales et structurales.

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Body size is widely recognized as an important factor affecting predator–prey relationships. Most fishes are ultimately gape-limited predators (e.g. Lawrence 1957; Werner 1977; Wankowski 1979), so size differences between predator and prey can limit prey consumption (Ivlev 1961; Werner 1977). Large size thus offers an important escape mechanism for prey of fishes (e.g. Vince et al. 1976; Kneib and Stiven 1982). However, direct and indirect effects of this type of interaction have seldom been documented at the population or assemblage level in systems where predator and prey are fishes (Parker 1971; Zaret and Paine 1973; Werner et al. 1983).

Besides being dependent on body size, the intensity of predation in an assemblage can change as physical conditions vary (Connell 1975). If prey can tolerate conditions that predators cannot, a period of environmental harshness can create local refuges by eliminating predators (Meffe 1984).

We focused on the interaction between central mudminnows (*Umbra limi*) and yellow perch (*Perca flavescens*) in small, northern Wisconsin lakes and the influence of the abiotic environment on this interaction. Fish assemblages in these shallow bog lakes are depauperate, with lakes containing (1) only mudminnows, (2) both mudminnows and perch, and (3) mudminnows, perch, and various minnows (Cyprinidae), bullheads (*Ictalurus* spp.), and/or other species (Tonn and Magnuson 1982; Rahel 1984). Earlier work with these *Umbra−Perca* assemblages documented a population-level dominance of perch over mudminnows (Tonn 1985). However, low oxygen concentrations during some winters can reduce perch populations whereas mudminnows are well adapted for under-ice survival in hypoxic waters (Klinger et al. 1982; Magnuson et al. 1983). Because winterkill is often size selective, with large fish being more vulnerable (Casselman and Harvey 1975), small mudminnows might temporarily enjoy reduced predation pressure if piscivory by small, surviving perch is gape limited. Thus, body size and abiotic conditions could operate together and alter any interactions between the two species.

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We examined the hypothesis that predation structures *Umbra−Perca* assemblages by comparing densities and size structures of mudminnow populations in lakes with and without perch and by monitoring changes in the two species' populations in six lakes over 6 yr. Major winterkills of perch occurred in two of the six lakes and we followed the responses of both species. Temporal changes within single assemblages thus complemented the spatial patterns observed across assemblages.

To evaluate hypotheses generated by the field studies, we performed a laboratory predation experiment. It was designed to measure the effects of the predator−prey relationship at the population level, using treatments based on population size structures observed in one lake at various times after a winterkill.

Field Studies

Methods

Five of our study lakes (Camp 2, Jude, Junnie, 6-7, and 33-13; Vilas and Oneida counties, Wisconsin) were small (<7 ha), shallow (<7 m), dystrophic seepage lakes characterized by stained, acidic waters, soft organic bottoms and floating *Sphagnum*-mat shorelines (Tonn 1985). A sixth, Mystery Lake (Vilas County), was slightly larger (8.5 ha), circumneutral, and more productive, with an outlet and an intermittent inlet (Tonn and Magnuson 1982). Mystery and Camp 2 had extensive beds of macrophytes throughout whereas Jude, Junnie, 6-7, and 33-13 had only sparse patches of submergent and floating-leaf vegetation along their edges. Lakes 33-13 and 6-7 contained only central mudminnows. Jude and Junnie had both mudminnows and yellow perch, and Camp 2 had mudminnows, perch, and a small population of golden shiners (*Notemigonus chrysoleucas*). Mystery's *Umbra*−cyprinid assemblage was richer (7−12 species) and more temporally variable in composition, but included populations of both mudminnows and perch (Tonn and Magnuson 1982; W. M. Tonn and C. A. Paszkowski, unpubl. data).

Biomass densities and size−frequency distributions of mudminnow and perch populations were measured five to eight times per lake between 1978 and 1983. For detailed descriptions of sampling protocols, see Tonn and Magnuson (1982) and Tonn (1985). Fish were caught in small fyke nets or minnow traps (both with 5-mm^2 mesh); both types of gear were set for about 24 h on lake bottoms in water ≤3 m deep (48 h and some midwater traps were used in 1978).

We estimated populations during 7- to 15-d censuses by the multiple Petersen-type mark−recapture method (Ricker 1975), whenever sufficient numbers of fish were recaptured (see below). Crude population densities could be calculated by dividing the population estimates by total lake area, but Tonn (1985) concluded that central portions of the lakes >3 m were unsuitable habitat, significantly underused by these populations; therefore, more meaningful ecological densities were calculated using only the portions of the lakes ≤3 m. These portions comprised 68−100% of total areas (Tonn 1985).

Due to the assumptions and limitations of the mark−recapture method (Ricker 1975), we calculated population densities from catch-per-unit-effort equations whenever we did not obtain at least three recaptures on at least 3 sampling days during a census. This occurred for mudminnow populations in Mystery, Camp 2, and Junnie, perch in Mystery, and for all populations sampled in 1978 and 1983. The following regression equations were determined from mean trap and net catches and mark−recapture estimates for those sampling periods in the five *Umbra−Perca* study lakes that had both catch-per-unit-effort and adequate mark−recapture data:

$$\log\,(\text{mudminnow density}) = 2.456 + 1.856 \times \log\,[(\text{mudminnow}\cdot\text{minnow trap pair}^{-1}) + 1]$$

$$R^2 = 0.88, \quad N = 15, \quad P < 0.01$$

$$\log\,(\text{perch density}) = 2.433 + 0.495 \times \log\,(\text{perch}\cdot\text{fyke net}^{-1})$$

$$R^2 = 0.44, \quad N = 22, \quad P < 0.01.$$

To convert numerical densities into biomass densities, and to obtain size−frequency distributions, samples of fish were weighed (nearest 0.01 g, live, wet mass) and measured (nearest 1 mm, total length (TL)) during each seasonal census. Mean census-period sample sizes for mudminnow and perch populations were 180 and 254 individuals, respectively. Eight-millimetre intervals, chosen arbitrarily via computer analyses, were used in constructing length−frequency distributions. Daily estimates were $\log_{10}$ transformed when computing mean biomass densities for each census.

To examine if, and how, perch affected mudminnow populations, we compared patterns of mudminnow density and size distribution in mudminnow-only and mudminnow−perch assemblages. Mean densities and total lengths were computed for each lake by averaging log-transformed census values for each year and then averaging among years. We also examined temporal patterns of density and lengths within lakes (Jude and Mystery) that experienced major winterkills of perch during 1978−83 by comparing census means from before and various times after the disturbances using *t*-tests.

Results and Discussion

Spatial patterns

From 1978 to 1983, combined mudminnow−perch biomass densities in Mystery, Camp 2, Junnie, and Jude lakes ($\bar{x} = 40.0\ \text{kg}\cdot\text{ha}^{-1}$, SD = 13.7, range = 22.5−55.7) were similar to mudminnow-only densities in 6-7 and 33-13 ($\bar{x} = 47.1\ \text{kg}\cdot\text{ha}^{-1}$, SD = 13.4, range = 37.6−53.6) (Fig. 1; see also Tonn 1985). However, mudminnow densities were considerably lower in the four assemblages containing perch ($\bar{x} = 5.6\ \text{kg}\cdot\text{ha}^{-1}$, SD = 3.8, range = 1.7−8.9) (Fig. 1). In addition, mean total lengths of mudminnows from the four populations cooccurring with perch ($\bar{x} = 78.6$ mm, SD = 8.2,

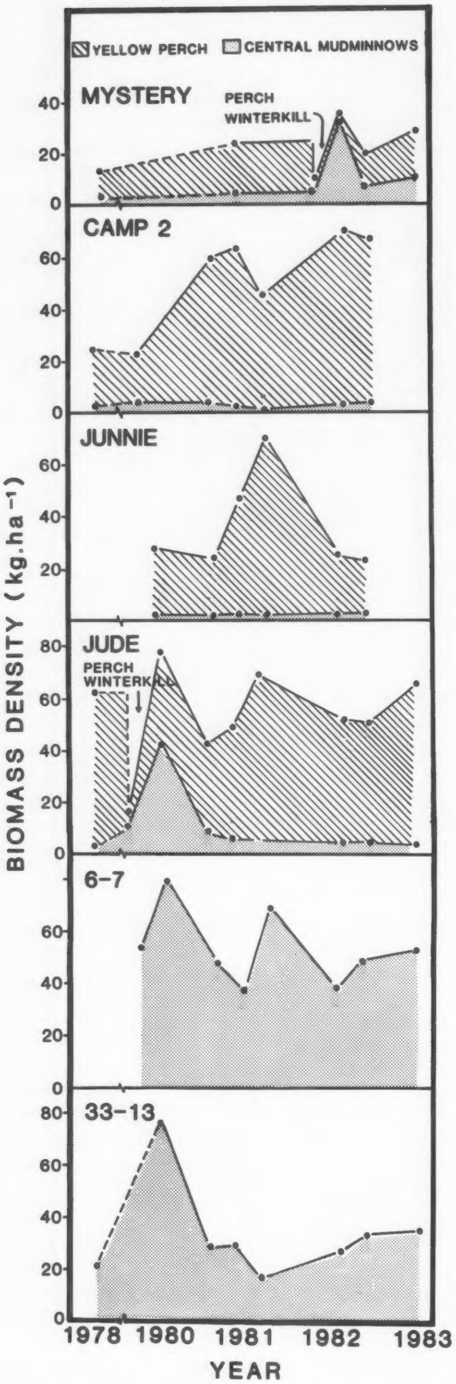

FIG. 1. Individual population and summed *Umbra–Perca* assemblage biomass densities in six northern Wisconsin lakes during 1978–83. Densities were calculated from mark–recapture estimates and catch-per-unit-effort relations, combined with mass–frequency distributions.

range = 69.5–87.2) were 21% larger than lengths of mudminnows found in the absence of perch ($\bar{x}$ = 65.1, SD = 3.0, range = 63.0–67.2). The low densities of mudminnow populations and the rarity of small mudminnows in mudminnow–perch assemblages suggested that population dominance by perch was caused by a size-dependent interaction, e.g. size-limited predation.

The dominant populations, mudminnows in mudminnow-only assemblages and perch where the two species cooccurred, varied considerably in density, both within and among years (Fig. 1; Tonn 1985). However, except for brief increases in abundance following winterkills of perch in Jude and Mystery, mudminnow population densities in the presence of perch were consistently low, lacking the large recruitment-related fluctuations observed in mudminnow-only lakes and perch populations.

During the 1979–80 winter, an early freeze and lengthy, continuous snow cover reduced concentrations of dissolved oxygen in Jude Lake (W. M. Tonn and C. A. Paszkowski, pers. obs.); the oxygen level at 1 m was 1.0 $mg \cdot L^{-1}$ in late February. At ice-out, large numbers of dead adult perch were observed on the lake surface (L. Radloff, Route 1, Boulder Jct., WI 54512, pers. comm.). Based on catch-per-unit-effort estimates in July 1980, only 300 adult (≥2 yr old) perch survived the winterkill, a 96% reduction compared with the estimated 6800 adults present in 1978. Because mudminnows have a number of behavioral and physiological mechanisms permitting survival under low winter oxygen concentrations (Mills 1972; Klinger et al. 1982; Magnuson et al. 1983), their population was not reduced; in fact, numbers were higher (4800) in the spring of 1980 than in 1978 (1000).

In July, large numbers of yearling mudminnows and perch were recruited to our sampling gear, indicating that juveniles from the 1979 year-classes were repopulating the lake. Because Jude has no inlets or outlets, immigration was not a factor. Sampling during October 1980 revealed the greatest total numbers and biomass of fishes observed in Jude (Fig. 1); biomass density of mudminnows was 14 times greater than in 1978 (43 vs. 3 $kg \cdot ha^{-1}$). However, by September 1981, mudminnow biomass density had returned to prewinterkill levels (5.5 $kg \cdot ha^{-1}$), a significant reduction from the density in October 1980 (t = 11.3, df = 11, $P < 0.001$). Mudminnow biomass density remained low, similar to levels in Junnie and Camp 2, through May 1983 (Fig. 1). With rapid growth of individuals from the 1979 year-class and successful reproduction and recruitment following winterkill, the perch population also returned to a prewinterkill density in 1981, maintaining it for the remainder of the study.

Both before the winterkill of perch in Jude and following winterkill but before recruitment of the 1979 year-class, only 36% of the mudminnow population was composed of small (<76 mm) individuals (Fig. 2). This pattern was similar to that of other mudminnow populations that cooccurred with perch (Camp 2 and Junnie; $\bar{x}$ = 26%, SD = 9, range = 10–46). However, successful recruitment of the 1979 year-class resulted in a predominance (58–86%) of small mudminnows in Jude the first year after winterkill (July 1980 – May 1981). During this period the proportion of the population <76 mm was similar to those in mudminnow-only assemblages (63–67%). At the same time, nearly all (91–99%) of the perch were small (<132 mm; Fig. 2).

These temporal population patterns complemented spatial patterns, and also suggested the operation of size-limited

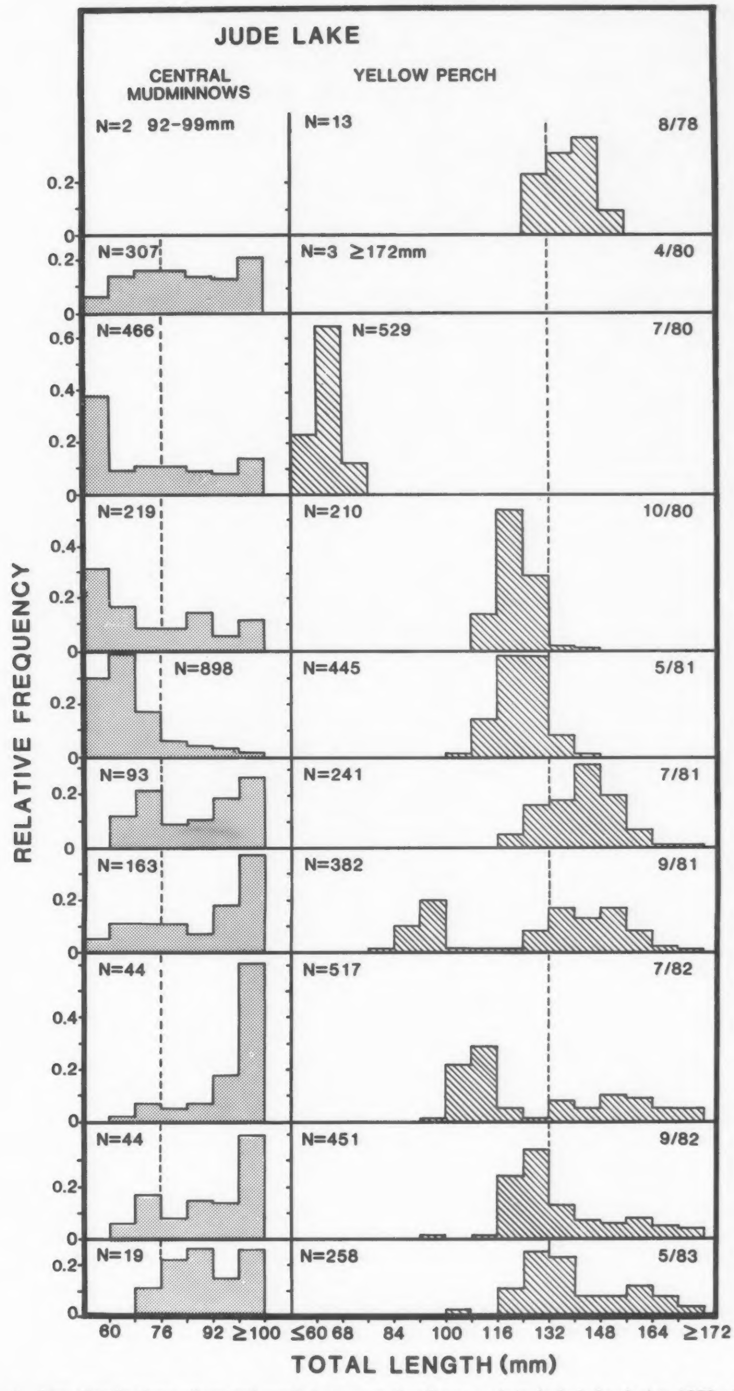

FIG. 2. Size distributions of central mudminnows and yellow perch in Jude Lake during 1978–83. A winterkill of perch occurred in early 1980; the April 1980 distributions are extrapolations based on nonyearlings in the July 1980 sample, and were assumed to represent populations at ice-out. Broken vertical lines represent arbitrary divisions (76 mm for mudminnows, 132 mm for perch) between small and large fish.

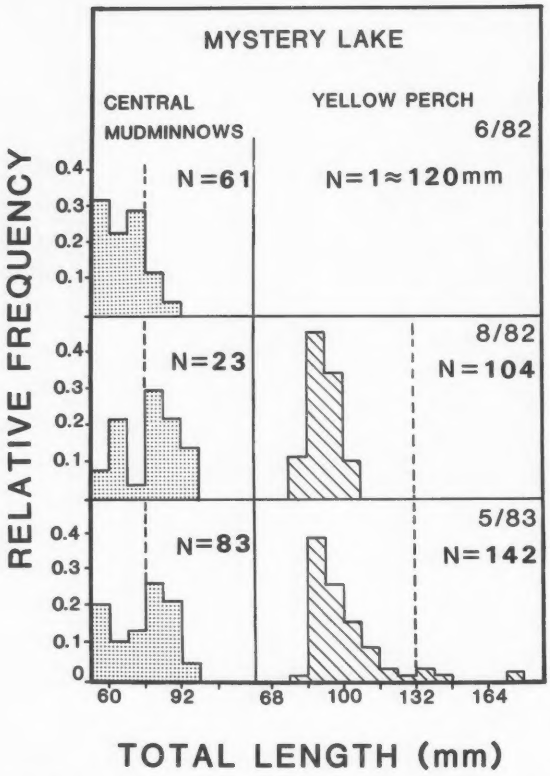

FIG. 3. Size distributions of central mudminnows and yellow perch in Mystery Lake following the 1982 winterkill.

predation: undisturbed perch populations regulate mudminnow densities and size structures by preying heavily on small mudminnows whereas large mudminnows exceed the upper size limit for prey of the perch and thereby attain a refuge from predation. Following severe winterkills that selectively remove large perch, successful recruitment of mudminnows occurs because surviving perch are initially too small to prey significantly on yearling mudminnows.

Between May and July 1981, 79% of the perch in Jude grew into size-classes ≥132 mm, and in the absence of winterkill, large sizes remained important (40−70%) through 1983. Simultaneously, the proportion of the mudminnow population <76 mm decreased from 86 to 34% whereas the proportion of very large individuals (≥92 mm) increased dramatically (4 to 44%; Fig. 2). The predominance of large mudminnows and the paucity of small sizes continued through 1983. After July 1981, the mudminnow population size structure in Jude was again similar to those in Junnie and Camp 2, but differed from those in 33-13 and 6-7.

We propose that a brief but intense period of size-limited predation by newly piscivorous perch began sometime after May 1981 and was essentially complete by July. We qualitatively examined diets of perch in January, May, July, and September of 1981; thus, our sampling missed this period. However, we did find a small (50−55 mm) mudminnow in the stomach of a 140-mm perch taken in July and mudminnow scales in a perch stomach in September whereas no mudminnows were found in stomachs from January or May. While not sufficient, this does provide direct evidence of predation and is consistent with the nature and timing of the proposed predator−prey interaction. After July 1981, larger perch were continuously present, the mudminnow population density was low, and small mudminnows remained rare.

Although our sampling effort was less intense, we also observed mudminnow and perch populations before and after a 1982 winterkill of large perch and other species in Mystery Lake (M. Hoff, Wis. Dep. Nat. Res., Box 440, Woodruff, WI 54568, pers. comm.). The general responses of the two populations were similar to those seen in Jude. Perch numbers and biomass density were extremely low in the spring after winterkill, but high survival and growth by the 1981 year-class resulted in recovery within a year (Fig. 1). Mudminnow numbers and biomass density increased sharply (from 4.0 to 31.5 $kg \cdot ha^{-1}$) with the reduction in perch, but again this increase was temporary. Before winterkill, perch and mudminnow size structures were qualitatively similar to other cooccurring populations (W. M. Tonn and C. A. Paszkowski, pers. obs.). After winterkill, size structures of the populations (Fig. 3) were comparable with those in Jude in their first postwinterkill year. Small but fast-growing yearlings of the 1981 cohort dominated (94−100%) the perch population whereas the mudminnow population had a relatively large proportion (54%) of small (<76 mm) fish. Only the beginnings of postwinterkill recovery occurred in Mystery by 1983 (Fig. 1 and 3).

As in other systems (Svärdson 1976; Skud 1982), the dominant mudminnow-only and perch populations appeared to be regulated primarily by abiotic factors and/or intraspecific processes, and showed considerable seasonal and annual variations in density. Mudminnow populations cooccurring with perch were subdominant, apparently regulated by interspecific interactions, and generally failed to show major temporal variations in density unless temporarily released by winterkill.

Laboratory Predation Experiment

Our interpretation of the spatial and temporal patterns of population density and size structure, based on a size-related predator−prey relation between perch and mudminnows, rests on two assumptions: (1) small mudminnows (<76 mm) are more vulnerable to perch predation than large mudminnows and (2) large perch (≥132 mm) are more effective predators on mudminnows than are small perch. To examine these assumptions we performed a laboratory experiment in which mudminnow populations with different size structures were combined with perch of different sizes. Size structures of our experimental populations were based on those observed for Jude Lake populations at specific times following the 1980 winterkill.

Materials and Methods

We used two fiberglass tanks, 1.83 m in diameter and 80 cm deep, with 6−8 cm of bottom sand. To simulate submergent vegetation, we added a low density (21 $stems \cdot m^{-2}$) of plastic aquarium plants in alternating patterns of clumps and scattered individuals. To simulate four pond lilies, strips of nylon rope were weighted at one end with the free end tied to 30 × 10 cm pieces of styrofoam and distributed around one clump of plastic plants. Water temperature was 13−18°C and the light regime was 8 h light : 16 h dark.

Each treatment began with 100 mudminnows and 8 perch. Mudminnows were obtained from Lakes 33-13 and 6-7 and perch from Jude Lake. All fish were measured (TL, nearest

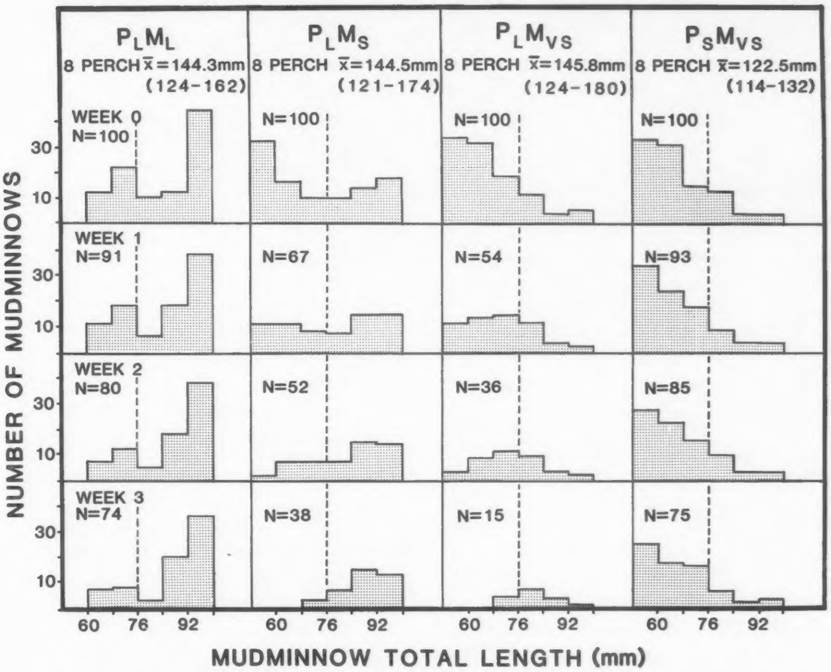

FIG. 4. Mean initial lengths (and ranges) of yellow perch, and numbers and size distributions of initial mudminnow populations (week 0) and populations surviving after each week in the four treatments of the laboratory predation experiment. P_L = large perch; P_S = small perch; M_L = large mudminnows; M_S = small mudminnows; M_{VS} = very small mudminnows. Broken vertical lines divide mudminnows into small (<76 mm) and large (≥76 mm) individuals.

0.5 mm) and weighed (wet mass, nearest 0.01 g) immediately before they were added to the tanks to create specific size distributions (see below). Mudminnows were added 24−48 h before perch. At weekly intervals the perch and surviving mudminnows were captured, measured, and weighed. The two species were held separately overnight in small tubs before being returned to the experimental tanks, which had been drained, cleaned, and filled with fresh water. During the course of the experiment one mudminnow died from unknown causes, apparently unrelated to perch attacks, and was replaced with an equal-sized individual. Several dozen caddisfly larvae (Trichoptera) and dragonfly naiads (Odonata), common items in the diets of both fishes (W. M. Tonn, unpubl. data), were also provided as invertebrate prey.

Four treatments, representing different combinations of two perch and three mudminnow size distributions (Fig. 4), were run for 3 wk each. Treatments P_LM_L, P_LM_S, and P_LM_{VS} varied mudminnow sizes (large, small, and very small, based on July 1981, October 1980, and May 1981 sizes in Jude Lake, respectively) but kept perch sizes constant (large), and thus examined how the initial size distribution of prey affected their subsequent survival and size distribution. Treatments P_LM_{VS} and P_SM_{VS} varied perch sizes (large and small, based on July and May 1981 sizes in Jude Lake, respectively) but kept initial prey sizes constant (very small), and thus examined the effects of predator size distribution on predation patterns. Based on our proposed mechanisms, we predicted that (1) mudminnow survival would be greater as we increased initial average mudminnow size ($M_{VS} < M_S < M_L$), (2) changes in size structure of mudminnow populations would be greater as we decreased initial average mudminnow size ($M_L < M_S < M_{VS}$), and (3) mudminnow survival would increase as average perch size decreased ($P_L < P_S$).

Total survival of mudminnows, among all size-classes combined and within individual size-classes, were compared between treatment pairs by the Mantel−Haenszel test (Miller 1981), with the MH test statistic approximating a χ^2 distribution. To examine the predation rate within each treatment, through time, we compared observed survivorship with an exponential model that assumes a constant predation rate (Miller 1981). Changes in size distributions of mudminnows within and between treatments were evaluated by Kolmogorov−Smirnov tests.

Results and Discussion

The behavior of both species in the tanks helped explain population-level results. Mudminnows most frequently rested on or near the bottom, especially among plants or along aquaria walls. Often they congregated in groups of a dozen or more fish. Perch were more active, circling the tanks singly or in small groups (two to three individuals) in the bottom half of the water column. Perch constantly attempted prey captures during daylight hours. An individual perch would slowly approach head-on to within a few centimetres of a mudminnow, rotate its entire body 90° in the horizontal plane so that the widest axis of its open mouth paralleled the widest (dorsoventral) axis of the mudminnow, and lunge at the mudminnow's head. While mudminnows usually darted away as perch oriented or lunged, all observed ingestions occurred head first. Cannibalism was never observed.

These predatory tactics were consistent with other field and laboratory observations of piscivory in *Perca* spp. (Deelder 1951; Hoogland et al. 1956; Nursall 1973; W. M. Tonn and C. A. Paszkowski, pers. obs.). Unlike more specialized piscivores, e.g. northern pike (*Esox lucius*), perch generally capture fish prey head first because they are unable to manipulate them after capture. With more active, openwater fishes, e.g. cyprinids, this behavioral/morphological restriction presents a nearly insurmountable barrier to predatory success for individual perch, and piscivory almost always requires active pursuit and "pack hunting." In contrast, the sedentary behavior of mudminnows makes them vulnerable to predation even by individual perch.

As predicted, survival of mudminnows (Fig. 4) was significantly greater in P_LM_L where the initial prey population contained a predominance of large individuals, than in P_LM_S (Mantel−Haenszel test; MH = 27.5, df = 1, $P < 0.001$) or P_LM_{VS} (MH = 73.6, df = 1, $P \ll 0.001$), where small mudminnows initially predominated. Consistent with this pattern, survival was also greater in P_LM_S than in P_LM_{VS} (MH = 11.7, df = 1, $P < 0.001$). Within each of the three treatments, predation rate was constant over time, i.e. observed survival did not differ ($P > 0.05$) from an exponential model.

These results were thus consistent with the first of our basic assumptions regarding the predator−prey interaction that small mudminnows are more vulnerable to perch predation than large ones. Overall differences in survival were due to initial differences in the size structure of experimental mudminnow populations, i.e. to the proportion of prey in size-classes vulnerable to a population of size-limited predators.

These significant, internally consistent results among the three experimental prey populations (M_L, M_S, M_{VS}) suggested that the three populations of similar-sized predators (P_L) were behaving comparably. Indeed, survival did not differ significantly within size-classes of mudminnows across treatments ($P > 0.05$), e.g. mudminnows 68−75 mm long survived similarly with all three groups of P_L. The only exception was the higher survival of fish 60−67 mm long in M_L during the third week (vs. M_S: MH = 13.0; vs. M_{VS}: MH = 14.4, df = 1 and $P < 0.001$ for both comparisons). Observations suggested that small mudminnows in M_L were using congregations of large individuals, which simply were not present in the other two populations, as structural refuges.

Size distribution patterns were also consistent with our predictions (Fig. 4). The size distribution of population M_L did not change significantly over the 3-wk experiment (Kolmogorov−Smirnov test, $P > 0.05$). By the end of the second week, however, the size distribution of mudminnows in M_S and M_{VS} differed significantly from initial distributions ($P < 0.01$). These differences were the result of heavy predation on small size-classes and minimal mortality among larger individuals.

Differences between P_LM_{VS} and P_SM_{VS} were consistent with our second assumption that large perch are more effective as mudminnow predators than are small perch. Survival of mudminnows was much higher in P_SM_{VS} than in P_LM_{VS} (MH = 80.3, df = 1, $P \ll 0.001$), and the size structure of the mudminnow population in P_SM_{VS} did not change significantly (Kolmogorov−Smirnov test, $P > 0.05$; Fig. 4). Within each of the three large size-classes of mudminnows (≥76 mm), survival did not differ between P_LM_{VS} and P_SM_{VS} (Mantel-Haenszel tests, $P > 0.25$). However, mudminnow survival was significantly greater in P_SM_{VS} for the three small size-classes ($P < 0.001$). As in the other treatments, observed survival in P_SM_{VS} did not differ ($P > 0.05$) from an exponential model.

That large perch were more successful predators was also reflected in the pattern of biomass increase among individual perch. Change in mass during the experiment was positively and significantly related to perch length: change in mass (g) = −185.1 + 88.6 [$\log_{10}$ (initial TL (mm))]; $R^2 = 0.839$, $N = 16$, using P_LM_{VS} and P_SM_{VS}. The *x*-intercept, i.e. the length at which there was no change in mass, occurred at 123 mm; a 132-mm perch gained 2.67 g (about 13% of initial mass) over the 3-wk experiment.

The laboratory results were consistent with our hypothesis that small mudminnows had a temporary refuge from predation after winterkill because surviving perch were initially too small to be effective piscivores. Specifically, the comparison of P_LM_{VS} with P_SM_{VS} suggested that sufficient numbers of perch in Jude Lake had not attained the size (13−14 cm) necessary for significant piscivory on mudminnows vulnerable to our traps (>40 mm) by May 1981 (=P_S), but had attained this size by July (=P_L), some 16 mo after the winterkill. Our laboratory results also showed that large mudminnows (≥76 mm) are less vulnerable than small mudminnows to predation by perch of sizes typical of *Umbra−Perca* assemblages (Fig. 2).

Discussion

The significantly reduced densities and altered size structures of mudminnow populations cooccurring with perch, the complementary temporal responses of mudminnow densities and size structures to winterkill and subsequent recovery of perch, and the supporting laboratory experiment all indicate that size-limited predation by yellow perch plays a major role in organizing *Umbra−Perca* assemblages. Although we detected the intense operation of this regulatory mechanism for only a brief (2 mo) period in Jude Lake, we believe that it also contributes to the maintenance of structure in *Umbra−Perca* assemblages on a long-term basis.

As is often also true for competitive interactions (e.g. Johannes and Larkin 1961; Connell 1980), there was little opportunity to observe this dominant structuring mechanism in action during our 6-yr study. Under undisturbed conditions it was not obvious that a predator−prey interaction was structuring the assemblages. Only following winterkill of large perch did mudminnow populations respond with large increases in density and shifts in population size structure. Even if large perch had remained absent, the nature of the predisturbance interaction would still have remained unclear. Only by documenting the complete cycle of undisturbed state, response to disturbance, and postdisturbance recovery could we focus our hypothesis. Our laboratory experiment confirmed that size-limited piscivory by perch of sizes typical of undisturbed *Umbra−Perca* assemblages could cause the patterns we observed for mudminnow populations.

The overall intensity of piscivory and specific form and degree of selectivity depend on characteristics (e.g. size, morphology, behavior) of both predators and their prey (e.g. Ivlev 1961; Beyerle and Williams 1968; Moody et al. 1983). Ivlev concluded that piscivorous fish generally select the largest prey that they can successfully ingest. Foraging cost-curves tend to confirm this conclusion; optimal prey sizes typically occur just below assymptotic rises in cost/benefit relations (Werner

1974, 1977; Gillen et al. 1981). Our findings are consistent with published predator–prey size relations for Eurasian perch (*P. fluviatilus*). Popova (1967, fig. 4) indicated that the maximum prey size of 150-mm perch was approximately 70 mm; this maximum increased sharply for perch between 150 and 200 mm, after which it stabilized around 130 mm. Zubenko (1982) reported the average prey size of 121- to 180-mm perch to be 44–60 mm, depending on the prey species. Our laboratory experiment showed that for yellow perch 121–180 mm TL, mudminnows <76 mm were significantly more vulnerable to predation than larger fish, a result consistent with field observations.

How are mudminnows able to persist with perch at low but relatively stable densities (e.g. in Camp 2, Junnie)? Long-term coexistence would be impossible if size-limited predation alone was operating. Although mudminnows can exceed the upper prey size of yellow perch in these assemblages, large individuals that are invulnerable to predation eventually die; their replacements must come from the small, vulnerable size-classes (Connell and Sousa 1983).

A number of other escape mechanisms may help mudminnow populations persist. Large cohorts of yearling mudminnows recruited to our gear in Jude and Mystery lakes following winterkills of perch, indicating that mudminnow populations can respond quickly to unpredictable temporal refuges. It also indicated that a substantial pool of young-of-the-year mudminnows had survived even in the presence of large perch. Spatial and/or structural refuges, combined with an element of chance related to low densities of large piscivorous perch due to stunting (W. M. Tonn and C. A. Paszkowski, pers. obs.), may also contribute to coexistence. The use of structural refuges was suggested by the fact that in September 1982, mudminnows were significantly concentrated within 2 m of the floating bog mat in Jude Lake in the presence of large perch, but not in 33-13, a mudminnow-only lake (Tonn 1985). Clady (1974) suggested that mudminnows also relied on spatial refuges to avoid predation by smallmouth bass (*Micropterus dolomieui).*

We have presented field and laboratory evidence that size-limited predation is an ecological mechanism important in the organization of *Umbra–Perca* fish assemblages. Whereas species-specific winterkill may have a direct regulatory role, we examined how it interacted with the predator–prey relationship and modified the intensity of predation. From our studies of these six assemblages over 6 yr, we agree with Paine (1976) that the complexities of natural systems, arising from unpredictable as well as predictable events, "should serve as a *caveat* to those willing to generalize about community structure based on single glimpses that ignore temporal and regional variations in the dynamics." As a result, we believe that an understanding of natural assemblages will not be reached solely by short-term studies, experimental or otherwise.

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Modification de la bioaccumulation du sélénium chez *Mytilus edulis* en présence du mercure organique et inorganique

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L'étude de la bioaccumulation simultanée du sélénium et du mercure chez la moule *Mytilus edulis* en présence de TiO_2 comme agent porteur a permis de mettre en évidence l'existence d'une interaction entre ces deux éléments. On a mesuré les vitesses de bioaccumulation du sélénite dissous (Na_2SeO_3) et du sélénium organique adsorbé ($(C_8H_7O_2Se)_2$) et on a déterminé les effets de la présence du mercure ($HgCl_2$ et $[(CH_3Hg)_3O]OH$) dans le milieu. Les moules de taille 3,6 ± 0,2 cm ont éte réparties dans neuf bassins de contamination avec une circulation en continu d'eau de mer et ont été soumises à des concentrations de 50 $\mu g\ Se \cdot L^{-1}$ en sélénium organique ou inorganique pendant des périodes de 15 à 50 jours. Certains bassins furent en même temps exposés à des fortes concentrations de 3,0 et de 30 $\mu g\ Hg \cdot L^{-1}$ en mercure organique et inorganique respectivement. Les moules accumulent lentement le sélénium inorganique (0,12 $ng\ Se \cdot g^{-1} \cdot d^{-1}$) administré seul tandis que le sélénium organique seul n'est pas accumulé. Quand 30 $\mu g\ Hg \cdot L^{-1}$ de mercure inorganique sont ajoutés à la circulation d'eau, l'accumulation du sélénium inorganique double sa valeur (0,24 $ng\ Se \cdot g^{-1} \cdot d^{-1}$) alors que cette vitesse est triplée (0,40 $ng\ Se \cdot g^{-1} \cdot d^{-1}$) si on ajoute du méthyl mercure à une concentration de seulement 3,0 $\mu g\ Hg \cdot L^{-1}$. Même le sélénium organique adsorbé semble devenir biodisponible en présence du méthyl mercure et son taux passe à 0,15 $ng\ Se \cdot g^{-1} \cdot d^{-1}$. Cependant, le phénomène n'est pas réciproque et la présence du sélénium n'a pas d'effet sur les vitesses d'accumulation du mercure quelle que soit la concentration et la nature du produit. Aucun effet toxique n'a été observé pour le sélénium seul mais la toxicité du mercure a été évidente dans tous les cas. Le sélénium ne montre aucun des effets antagonistes déjà observés chez diverses autres espèces animales.

Studies of the simultaneous bioaccumulation of selenium and mercury in the blue mussel, *Mytilis edulis*, in the presence of TiO_2 as carrier have shown that there is an interaction between the two elements. We measured the bioaccumulation rates of dissolved selenite (Na_2SeO_3) and adsorbed organic selenium ($(C_8H_7O_2Se)_2$) and determined the impact of the presence of mercury ($HgCl_2$ and $[(CH_3Hg)_3O]OH$) in the environment. Mussels measuring 3.6 ± 0.2 cm were distributed in nine contamination tanks with continuously circulating seawater and were exposed to organic or inorganic selenium at a concentration of 50 $\mu g\ Se \cdot L^{-1}$ for periods of 15–50 d. Some of the tanks were simultaneously exposed to high concentrations of organic and inorganic mercury (3.0 and 30 $\mu g\ Hg \cdot L^{-1}$, respectively). When mercury was not present, the mussels accumulated the inorganic selenium at a slow rate (0.12 $ng\ Se \cdot g^{-1} \cdot d^{-1}$), but did not accumulate the organic selenium. When inorganic mercury was added to the water at 30 $\mu g\ Hg \cdot L^{-1}$, the accumulation rate of inorganic selenium doubled (0.24 $ng\ Se \cdot g^{-1} \cdot d^{-1}$), while it tripled (0.40 $ng\ Se \cdot g^{-1} \cdot d^{-1}$) when methyl mercury was added at 3.0 $\mu g\ Hg \cdot L^{-1}$. Even the adsorbed organic selenium seemed to become bioavailable in the presence of methyl mercury, and was accumulated at a rate of 0.15 $ng\ Se \cdot g^{-1} \cdot d^{-1}$. However, the phenomenon is not reciprocal, that is, the presence of selenium, no matter what its concentration or chemical nature, had no effect on the accumulation rate of mercury. No toxic effects were observed where selenium was administered alone, but the toxic effects of mercury were observed in all mussels exposed to it. Selenium showed none of the adverse effects previously observed in other animal species.

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L'interaction biochimique entre le mercure et le sélénium chez les mammifères terrestres a fait l'objet de nombreux travaux au cours de la dernière décennie (Magos et Webb 1980). Dans le milieu aquatique, des travaux récents ont montré l'existence probable d'une interaction mercure–sélénium en eau douce et la possibilité d'utiliser le sélénium a été suggérée pour réduire la présence du mercure dans l'ensemble d'un écosystème fluvial (Rudd *et al.* 1983; Rudd et Turner 1983; Turner et Swick 1983). Ainsi, l'addition de sélénium inorganique stabilise le mouvement du mercure dans les divers compartiments de la colonne d'eau, retarde le taux de bioaccumulation du mercure et diminue le rapport Hg/Se chez le brochet et la perchaude (Turner et Swick 1983). D'autre part, Klaverkamp *et al.* (1983) montrèrent qu'une forte concentration de sélénium inorganique (100 $mg\ Se \cdot L^{-1}$) a un effet protecteur apparent sur la toxicité du mercure chez des oeufs de truite (*Salmo gairdneri*). La bioaccumulation simultanée du mercure et du sélénium dans le foie des mammifères marins a été plusieurs fois discutée et revue par Pelletier (1985); l'importance du phénomène a été attribuée à un mécanisme naturel d'épuration que posséderaient ces organismes (Martoja et Martoja 1978). Une corrélation linéaire entre les concentrations en mercure et en sélénium a aussi été notée chez les poissons comme le merlan noir (*Makaira indica* Cuvier) (Mackay *et al.* 1975), le mullet (*Mullus barbatus* L.) (Leozio *et al.* 1982) et l'espadon (*Xiphias gladius*) (Freeman *et al.*

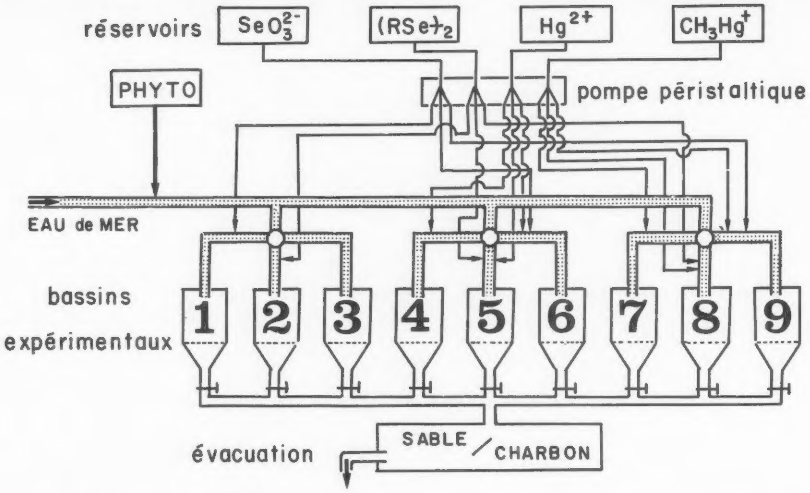


FIG. 1. Schéma de l'appareillage utilisé pour la contamination des moules. Les 9 bassins expérimentaux reçoivent les contaminants suivants : 1 : sélénite, 2 : sélénium organique, 3: témoin, 4 : mercure inorganique, 5 : mercure inorganique et sélénium organique, 6 : mercure inorganique et sélénite, 7 : méthyl mercure, 8 : méthyl mercure et sélénium organique 9 : sélénite et méthyl mercure.

1978). Enfin, un véritable antagonisme du sélénium sur la toxicité du mercure a été démontré par Gotsis (1982) chez l'algue *Dunaliella minuta*.

Dans certains milieux estuariens et côtiers, plusieurs espèces commerciales sont encore menacées par le mercure accumulé dans les sédiments, par exemple une contamination a été mise en évidence par Smith et Loring (1981) dans leur étude des sédiments du fjord du Saguenay (Canada). Les crevettes de la partie supérieure de ce fjord sont encore contaminées par le mercure environ 7 ans après la fermeture de l'usine apparemment responsable de la contamination (Cossa et Desjardins 1984). Aucune information n'est actuellement disponible relativement à la toxicité résultant de la présence simultanée du mercure et du sélénium chez ces organismes et à l'effet de l'un et de l'autre sur leur vitesse respective de bioaccumulation. Nous avons choisi *Mytilus edulis* pour cette étude à cause de sa large distribution dans l'est du Canada, sa facilité de maintien en captivité et l'abondance de la documentation scientifique à son sujet. Le but de notre travail est de fournir des données de base sur l'interaction mercure−sélénium chez *M. edulis* afin de permettre l'élaboration d'une hypothèse de mécanisme biochimique et d'évaluer la possibilité d'utiliser le sélénium dans un procédé industriel d'épuration des organismes contaminés.

Matériel et méthodes

Appareillage

L'ensemble de l'appareillage destiné à la contamination des moules est schématisé à la figure 1. L'eau de mer est filtrée à 0,5 μm et amenée par trois pompes à piston à un débit de $200 \text{ cm}^3 \cdot \text{min}^{-1}$ pour chacun des bassins expérimentaux. Les solutions mères de sélénium et de mercure sont entreposées dans quatre réservoirs de 11 L et sont amenées à la canalisation d'eau de mer par une pompe péristaltique Gilson® à multiples canaux. Les effluents des bassins de contamination sont filtrés sur un bac de gravier et de charbon avant d'être retournés à l'égoût du laboratoire. La couche de sable retient les particules contaminées et les fèces tandis que le charbon adsorbe le mercure libre. La photopériode fut de 12 h. Chaque bassin est constitué d'un tuyau en polyéthylène chargé de carbone soudé à un cône circulaire, du même matériau, formant le fond du

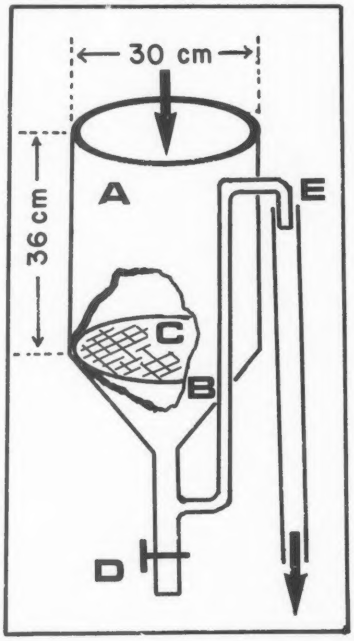
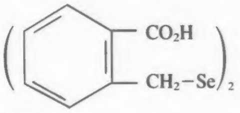


FIG. 2. Schéma de l'un des neuf bassins de contamination. A : réservoir, B : fond conique, C : support pour les moules, D : robinet de vidange permettant de recueillir les fèces et les détritus, E : déversoir pour ajuster le niveau du bassin.

TABLEAU 1. Concentrations des composés chimiques utilisés pour les mesures de bioaccumulation.

Composé	Formule chimique	Concentration dans les bassins expérimentaux
Chlorure mercurique	$HgCl_2$	30 $\mu g\ Hg \cdot L^{-1}$
Hydroxyde de méthyl mercure	$[(CH_3Hg)_3O]OH$	Série A : 30 $\mu g\ Hg \cdot L^{-1}$ Série B : 3,0 $\mu g\ Hg \cdot L^{-1}$
Sélénite de sodium	Na_2SeO_3	50 $\mu g\ Se \cdot L^{-1}$
Disélénium de bis(2-carboxybenzyl)		50 $\mu g\ Se \cdot L^{-1}$
Anatase	TiO_2	200 $\mu g \cdot L^{-1}$ (dans tous les bassins)

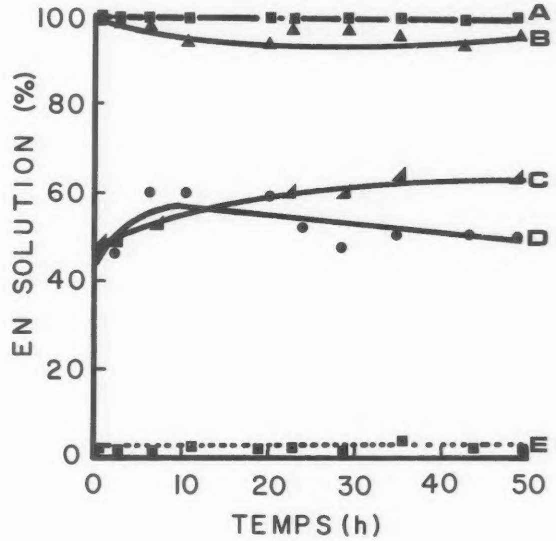


FIG. 3. Adsorption des différents composés chimiques sur l'anatase (TiO_2) à 25°C. A : Na_2SeO_3, B : $HgCl_2$, C : $[(CH_3Hg)_3O]OH$ 3,0 $\mu g \cdot L^{-1}$, D : $[(CH_3Hg)_3O]OH$ 30 $\mu g \cdot L^{-1}$, E : $(C_8H_7O_2Se)_2$.

bassin (figure 2). La tubulure et les fixations sont de Silicone® ou de Teflon®. L'utilisation de pièce métallique fut strictement évitée.

Conditions expérimentales

Les moules de taille 3,6 ± 0,2 cm (soit 1,0 ± 0,2 g de tissu mou) ont été échantillonnées sur un substrat rocheux à Pointe Mitis (48° 40′ N, 68° 02′ W) le long du littoral de l'estuaire du Saint-Laurent. Des études antérieures (Cossa et Bourget 1980; Picard-Bérubé *et al.* 1983) ont montré le faible niveau de contamination des moules à cet endroit. Au laboratoire, 156 moules furent placées dans chacun des bassins et acclimatées pendant 48 h avant le début de l'expérience. La température moyenne de l'eau de mer entrant dans les bassins durant toute la durée de l'expérience fut de 11,0 ± 1,5°C et la salinité moyenne de 22 ± 2 ‰. Pour chacun des jours d'échantillonnage, 12 moules furent prélevées de chacun des bassins et congelées pour les analyses ultérieures. Afin de maintenir constante la quantité de nourriture et de contaminants par rapport au nombre de moules dans chacun des bassins pendant toute la durée de l'expérience, 12 nouvelles moules isolées dans un filet de Nitex® furent placées dans chaque bassin pour remplacer les animaux prélevés. La série de prélèvement A avec le méthyl mercure (30 $\mu g\ Hg \cdot L^{-1}$) fut arrêtée après 15 jours à cause du taux très élevé de mortalité. Les bassins et la tubulure furent lavés à l'acide nitrique 10 % et la série B fut démarrée avec 3,0 $\mu g\ Hg \cdot L^{-1}$ sous forme de méthyl mercure.

Nourriture et contaminants

Les moules furent nourries avec l'algue *Phaeodactylum tricornutum* élevée en monoculture (Guillard 1975). La suspension de cellules fut pompée dans la canalisation d'eau de mer selon un flux d'environ 4 × 10^6 à 5 × 10^6 cellules par gramme de moule (tissu mou) et par jour. Les composés chimiques utilisés dans cette étude proviennent de Aldrich Chemical Co. et ont été utilisés sans autre purification. Le dérivé de sélénium organique, le diséléniure bis(2-carboxybenzyl) a été préparé et purifié selon la méthode de Klayman et Griffin (1973). Les solutions mères de mercure, de méthyl mercure, d'organodiséléniure et de sélénite ont éte préparées suivant une même procédure. La quantité requise du composé chimique fut d'abord dissoute dans exactement 1 L d'eau déionisée. Quelques gouttes de NaOH concentré furent nécessaires pour dissoudre le diséléniure. De très fines particules d'oxyde de titane formant une suspension colloïdale dans l'eau ont été ajoutées afin de procurer un support inerte aux composés peu solubles, de réduire les pertes par adsorption sur les parois et de permettre le transport des contaminants jusqu'aux bassins expérimentaux. Le pH fut ajusté à 8,0 pour aider à une bonne adsorption des composés sur les particules. La solution fut ensuite transférée au réservoir de polluant (figure 1) et diluée 10 fois avec de l'eau déionisée. Les solutions furent distribuées aux canalisations d'eau de mer avec les concentrations finales indiquées (tableau 1).

Méthodes analytiques

Pour chaque dosage, les tissus mous de cinq moules furent détachés des coquilles, rincés au-dessus d'un fin tamis avec de l'eau déionisée, essorés délicatement et pesés avec précision. L'acide nitrique concentré (15 cm^3) fut ajouté à 4,0 g d'échantillon et la digestion, effectuée à 25°C pendant au moins 12 h.

La solution jaune résultante fut ensuite utilisée pour la détermination du mercure (environ 1 cm^3) ainsi que pour l'analyse du sélénium (4 à 5 cm^3).

Le mercure total fut dosé par la méthode de Hatch et Ott (1968) en utilisant un spectrophotomètre sans flamme (Fisher modèle H-63). La limite de détection est de 0,05 $\mu g\ Hg \cdot g^{-1}$. Le sélénium organique (−II) et le sélénium (IV), excluant le sélénium (VI), furent analysés ensemble par chromatographie en phase gazeuse selon la méthode décrite par Cappon et Smith (1978, 1982) utilisant un chromatographe Perkin−Elmer modèle 900 équipé d'un détecteur à capture d'électrons (source au Nickel 63) et d'un intégrateur électronique Perkin−Elmer modèle LCI-100. Une colonne de verre de 2 m (2 mm d.i.) remplie avec 1,5 % OV-17 + 1,95 % QF-1 sur 80/100 Chromosorb W-HP a été utilisée en mode isothermique à 215°C. Le débit du gaz porteur (argon/méthane 15 %) a été ajusté à 60 $cm^3 \cdot min^{-1}$. Dans ces conditions, le temps de rétention du complexe 5-nitropiazsélinol fut de 4,05 ± 0,03 min. La limite de détection a été estimée à 0,5 $ng\ Se \cdot g^{-1}$ par Cappon et Smith (1978) et se trouve loin en-dessous des niveaux rapportés dans ce travail. Le pourcentage moyen de récupération à partir d'une solution aqueuse standard de Na_2SeO_3 fut de 90 ± 3 %.

Résultats

L'anatase comme support inerte

L'utilisation de fines particules de TiO_2 (4 nm) comme transporteurs de polluants constitue l'une des particularités expérimentales de notre étude. Quand une poudre d'oxyde de titane (anatase 99,9 %) est mélangée à de l'eau déionisée, il y a formation d'une dispersion colloïdale stable pendant plusieurs jours. Cette suspension a l'avantage d'offrir une très grande surface d'adsorption pour une quantité minimum de produit. TiO_2 est totalement insoluble dans l'eau et la toxicité des particules d'anatase n'a jamais été mentionnée pour des organismes aquatiques. L'anatase a donc été utilisé dans cette expérience comme support inerte pour transporter des composés insolubles ou ayant une forte tendance à l'adsorption, afin d'éviter le mieux possible les problèmes occasionnés par une perte considérable du mercure dissous tel qu'observé par Thain (1984). Pour des raisons similaires, Langston (1978) avait utilisé des particules d'alumine (Al_2O_3) pour transporter des BPC dans une étude de contamination chez des mollusques filtreurs. Ainsi, le dérivé organodiséléniure est presque insoluble à pH 8 et il devenait impossible de le distribuer de façon homogène dans le système d'alimentation en eau de mer. Il fut donc précipité lentement à partir d'une solution alcaline en présence d'une suspension colloïdale de TiO_2 afin d'obtenir une adsorption uniforme à la surface des microparticules. La suspension est demeurée homogène et a pu être pompée de façon régulière. La présence des particules de TiO_2 permet une adsorption importante du méthyl mercure qui diminue les risques de perdre le composé sur les parois du réservoir et dans la tubulure. Nous avons observé que la force ionique élevée de l'eau de mer provoque une désorption partielle du méthyl mercure, processus cependant beaucoup plus lent que le temps de résidence des particules dans le bassin de contamination. Par souci d'uniformité, l'anatase a aussi été ajouté aux solutions de mercure inorganique et de sélénite de sodium même si l'adsorption est faible dans les deux cas. A partir des données de la figure 3, on constate que le sélénium organique est entièrement adsorbé ou particulé, le sélénium inorganique ainsi que le mercure inorganique sont presque entièrement dissous et que le méthyl mercure est adsorbé à environ 50 % indépendamment des concentrations utilisées. Les solutions sont stables pour au moins 48 h, ce qui correspond au temps de remplacement des solutions mères.

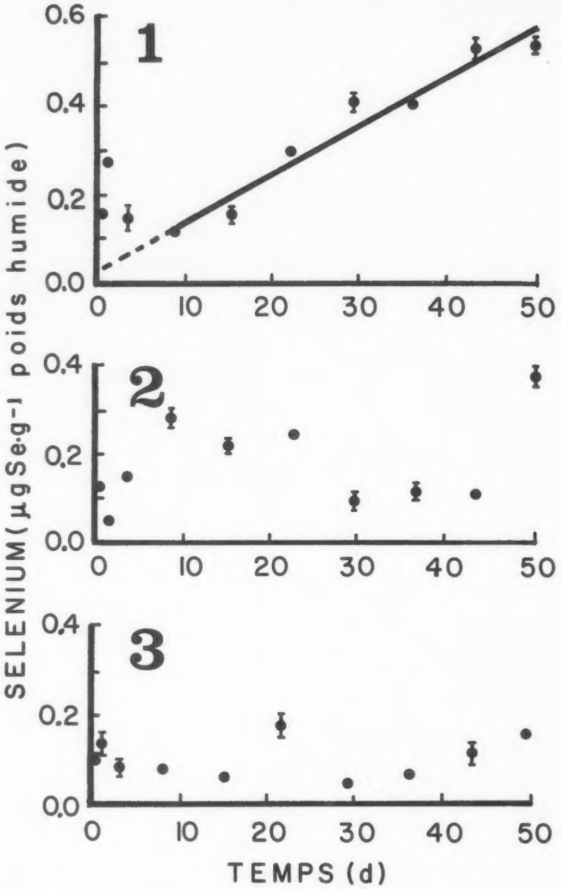


FIG. 4. Accumulation du sélénium chez *M. edulis*. Bassin 1 : Na_2SeO_3 seul (50 $\mu g\ Se \cdot L^{-1}$). Bassin 2 : $(C_8H_7O_2Se)_2$ seul (50 $\mu g\ Se \cdot L^{-1}$). Bassin 3 : témoin. Les valeurs représentent la moyenne ± σ de 3 déterminations.

Bioaccumulation du sélénium et du mercure

La figure 4 montre la bioaccumulation du sélénium seul chez *Mytilus edulis*. Le sélénium inorganique (bassin 1) s'accumule lentement et régulièrement après une latence d'environ 10 jours. Le taux de bioaccumulation (tableau 2) correspond à un facteur d'augmentation de la concentration de seulement 3 sur une période de 50 jours. Le retard à observer le début de l'accumulation peut être interprété comme une réaction immédiate du métabolisme qui réussit à éliminer l'excès de sélénium ou à bloquer l'assimilation pendant quelques jours malgré une concentration au moins 1000 fois supérieure à la concentration naturelle de l'eau de mer mesurée par Measures et Burton (1978). On note que le taux de bioaccumulation déterminé ici pour *M. edulis* est environ 50 fois plus lent que celui qui a été trouvé par Fowler et Benayoun (1976) chez *Mytilus galloprovincialis* pour une même concentration sur une période de

TABLEAU 2. Vitesses de bioaccumulation du mercure et du sélénium chez *M. edulis*.

Bassin	Composés chimiques	Mercure (μg Hg$\cdot$g$^{-1}\cdot$d^{-1})	Sélénium (μg Se$\cdot$g$^{-1}\cdot$d^{-1})	Mortalité cumulée[a]
1	Na_2SeO_3	—	$1{,}2 \times 10^{-2}$ (42)[a]	5 (50)
2	$(RSe)_2$ seul	—	—	5 (50)
3	Témoin	—	—	5 (50)
4	$HgCl_2$ seul	3,1 (50)[a]	—	20 (50)
5	$(RSe)_2$ et $HgCl_2$	2,8 (50)	—	22 (50)
6	Na_2SeO_3 et $HgCl_2$	3,1 (50)	$2{,}4 \times 10^{-2}$ (50)	18 (50)
7A	CH_3Hg^+ seul	3,0 (15)	—	84 (15)
8A	$(RSe)_2$ et CH_3Hg^+	3,6 (15)	—	78 (15)
9A	Na_2SeO_3 et CH_3Hg^+	4,0 (15)	—	35 (15)
7B	CH_3Hg^+ seul	1,4 (30)	—	62 (50)
8B	$(RSe)_2$ et CH_3Hg^+	1,4 (30)	$1{,}5 \times 10^{-2}$ (42)	52 (50)
9B	Na_2SeO_3 et CH_3Hg^+	1,6 (30)	$4{,}0 \times 10^{-2}$ (50)	56 (50)

[a] le nombre de jours utilisés pour les calculs est indiqué entre parenthèses.

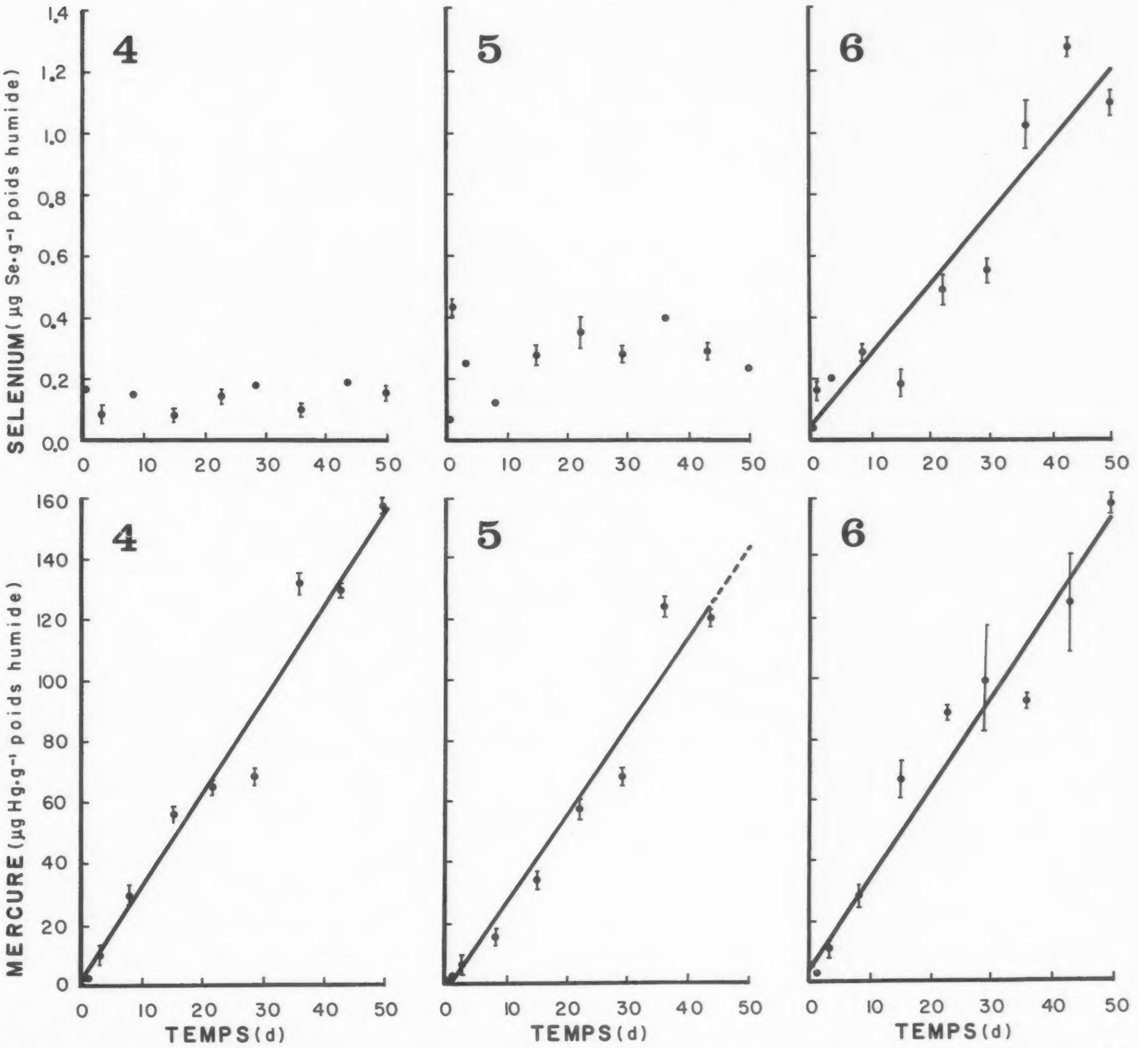


FIG. 5. Accumulation du sélénium et du mercure inorganique chez *M. edulis*. Bassin 4 : $HgCl_2$ seul (30 μg Hg$\cdot$L^{-1}). Bassin 5 : $(C_8H_7O_2Se)_2$ (50 μg Se$\cdot$L^{-1}) et $HgCl_2$ (30 μg Hg$\cdot$L^{-1}). Bassin 6 : Na_2SeO_3 (50 μg Se$\cdot$L^{-1}) et $HgCl_2$ (30 μg Hg$\cdot$L^{-1}).

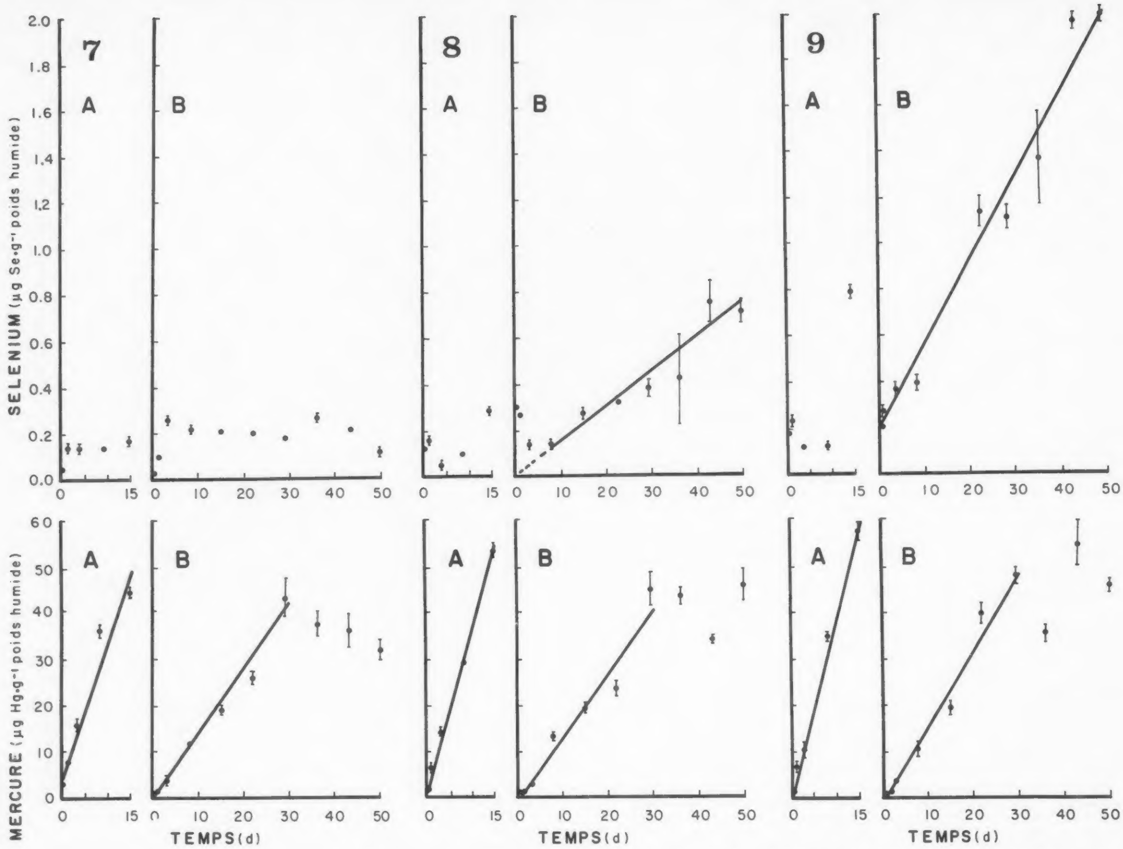


FIG. 6. Accumulation du sélénium et du méthyl mercure chez *M. edulis*. Bassin 7A : CH_3Hg^+ seul (30 $\mu g\ Hg \cdot L^{-1}$). Bassin 8A : $(C_8H_7O_2Se)_2$ (50 $\mu g\ Se \cdot L^{-1}$) et CH_3Hg^+ (30 $\mu g\ Hg \cdot L^{-1}$). Bassin 9A : Na_2SeO_3 (50 $\mu g\ Se \cdot L^{-1}$) et CH_3Hg^+ (30 $\mu g\ Hg \cdot L^{-1}$). Pour la série B, la concentration de CH_3Hg^+ a été réduite à 3,0 $\mu g\ Hg \cdot L^{-1}$ en conservant les mêmes concentrations de sélénium. Les valeurs représentent la moyenne ± σ de 3 déterminations.

21 jours. Des facteurs expérimentaux comme l'utilisation de bassins en circuit fermé et de moules plus grosses ainsi qu'une température et une salinité plus élevées peuvent contribuer à expliquer cette différence.

La figure 5 compare la bioaccumulation du mercure administré seul avec celles du sélénium et du mercure inorganique administrés simultanément. Les données du bassin 4 montre que le mercure seul s'accumule de façon régulière à un taux de 3,1 $\mu g\ Hg \cdot g^{-1} \cdot d^{-1}$ et ne provoque pas d'accumulation du sélénium naturellement contenu dans l'eau de mer utilisée ($\sim$0,05 $\mu g\ Se \cdot L^{-1}$). Dans le bassin 5, l'accumulation régulière du $HgCl_2$ à un taux de 2,8 $\mu g\ Hg \cdot g^{-1} \cdot d^{-1}$ ne semble pas interagir sur l'assimilation du dérivé organodiséléniure. La concentration moyenne du sélénium y est un peu plus élevée que dans le bassin témoin mais il peut s'agir d'une surévaluation de la concentration causée par des particules présentes dans le tractus digestif de la moule. L'accumulation du mercure dans le bassin 6 est aussi régulière que dans les deux autres (tableau 2) mais cette fois il y a évidence pour une augmentation importante du taux d'accumulation du sélénium inorganique. Le taux journalier de rétention ($2,4 \times 10^{-2}$ $\mu g\ Se \cdot g^{-1} \cdot d^{-1}$) est deux fois celui du sélénium administré seul (bassin 1). L'analyse de variance montre qu'il n'y a pas de différence significative entre les trois séries de données sur l'accumulation du mercure inorganique ($P \gg 0,05$). Ni le sélénium organique, ni le sélénium inorganique n'ont réussi à modifier l'accumulation de $HgCl_2$.

La figure 6 montre que la présence du méthyl mercure amplifie considérablement les effets de concentrations du sélénium déjà observés pour $HgCl_2$. Administré à une concentration de 30 $\mu g\ Hg \cdot L^{-1}$, le méthyl mercure s'accumule très rapidement dans les moules des trois bassins de la série A. L'analyse de variance montre que ces trois groupes de données ne sont pas significativement différents ($P > 0,05$). Selon les travaux de Fowler *et al.* (1978), l'accumulation du méthyl mercure chez *M. galloprovincialis* est de 2 à 3 fois plus rapide que celle du mercure inorganique sur une période de 35 jours. Nos résultats (tableau 2, bassins 4 et 7A) ne reflète pas véritablement cette tendance, cependant l'effet toxique du méthyl mercure dans notre expérience a certainement modifié l'activité de la moule alors que l'emploi d'un traceur radioactif en très faible concentration par Fowler et collaborateurs ne devait pas avoir perturbé l'activité normale du bivalve. D'autre part, la période de 15 jours fut trop courte pour véritablement estimer le taux de bioaccumulation du sélénium. Dans la série B, la concentration du CH_3Hg^+ a été réduite d'un facteur 10 et le taux d'accumulation a chuté d'un peu plus de la moitié. L'accumulation est assez régulière pendant les 30 premiers jours et les 3 groupes de valeurs ne sont pas significativement différents entre eux ($P \gg 0{,}05$). Cependant dans les 20 derniers jours de l'expérience, l'accumulation a pratiquement cessé malgré la poursuite de la contamination. Les analyses de sélénium du bassin 8B semblent montrer un début de bioaccumulation du sélénium organique à un taux de 1,5 $\mu g\, Se \cdot g^{-1} \cdot d^{-1}$. Le méthyl mercure aurait contribué à rendre le dérivé organodiséléniure au moins partiellement biodisponible. Pour le sélénium inorganique du bassin 9B, il a un taux d'accumulation presque deux fois élevé que dans le bassin 6 et quatre fois plus que dans le bassin 1. L'interaction du méthyl mercure y semble évidente d'autant plus que sa concentration est 10 fois plus faible que celle du $HgCl_2$ du bassin 6.

Discussion

Métabolisme du sélénium

L'absence de bioaccumulation du sélénium organique particulaire (bassin 2) semble indiquer que cette forme réduite du sélénium n'est pas directement biodisponible pour ce mollusque filtreur, même à une forte concentration. La molécule de diséléniure de bis(2-carboxybenzyl) (tableau 1) a été utilisée dans cette expérience parce que sa structure modélise assez bien la structure de la sélénocystine et des sélénoprotéines que l'on croit présentes dans la matière vivante (Carty *et al.* 1983). Les présentes données ne permettent cependant pas de déterminer si l'absence d'accumulation (ou la rapide élimination) est due à la structure chimique de la molécule ou à son caractère insoluble au pH de l'eau de mer. La non-utilisation de cette source de sélénium réduit par la moule pour son propre métabolisme semble indiquer que le cycle biogéochimique du sélénium (Shrift 1972) ne peut pas être court-circuité par l'utilisation directe du sélénium déjà réduit. La cycle du sélénium en milieu océanique a été récemment réévalué par Cutter et Bruland (1984). Les auteurs proposent une oxydation par étapes successives du sélénium organique en sélénite puis en sélénate. La possibilité de l'utilisation directe par les organismes du sélénium réduit n'a cependant pas été discutée. Donc il semble que le sélénium organique réduit doive retourner à l'état d'oxydation +IV ou même +VI avant d'être de nouveau introduit dans le cycle biologique. Cette hypothèse n'est pas en accord avec les résultats de Fowler et Benayoun (1976) qui indiquent que le sélénium s'accumule plus vite par la chaîne alimentaire (phytoplancton marqué) et que ce processus devrait donc jouer un rôle significatif dans l'accumulation du sélénium en milieu naturel. Cependant, il est possible que le sélénium transporté par le phytoplancton dans l'expérience de Fowler et Benayoun soit du sélénium inorganique simplement adsorbé à la surface des cellules et qu'il ne puisse pas être consideré de nature organique comme celui qui a été utilisé dans notre expérience.

Toxicité et antagonisme

Les effets toxiques du mercure ont été observés dans tous les cas. En présence de Hg^{2+} et CH_3Hg^+ (jusqu'à 50 $\mu g\, Hg \cdot L^{-1}$), la moule réduit sa vitesse de filtration et on observe une diminution progressive de la production de fèces (Watling et Watling 1982). Nous observons une augmentation importante de la mortalité après 30 jours de contamination. La présence du sélénium n'a pas modifié de façon significative la mortalité accumulée à la fin de l'expérience (tableau 2). La mortalité après 15 jours dans le bassin 9A est nettement inférieure à celles qui ont été retrouvées dans les deux autres bassins de la même expérience, et on serait tenté d'attribuer cette différence à la présence du Na_2SeO_3. Cependant, une telle conclusion est prématurée parce que nous ne disposons que d'une seule donnée finale et que la mortalité n'a pas été déterminée dans les jours précédents. Le phénomène n'est d'ailleurs pas confirmé dans la série B. On peut expliquer l'arrêt de la bioaccumulation du CH_3Hg^+ dans les bassins 7 surtout, et aussi 8 et 9, de la série B par l'arrêt presque complet de la filtration dû à l'intoxication. Aucun effect toxique n'a été observé dans les bassins recevant uniquement du sélénium et le taux de mortalité demeure très faible dans tous les cas (tableau 2).

L'hypothèse d'un antagonisme sélénium−mercure chez le rat de laboratoire a d'abord été proposé par Parizek et collaborateurs (Parizek et Ostadalova 1967; Parizek *et al.* 1971). Par la suite, plusieurs travaux sont venus confirmer les premières observations (Magos et Webb 1980) et des hypothèses mécanistiques ont été proposées (Ganther 1977; Rabenstein 1978; Ridlington et Whanger 1981). On observe généralement trois effets antagonistes chez les animaux de laboratoire : (1) le sélénium réduit considérablement les effets toxiques du mercure inorganique et du méthyl mercure; (2) la rétention de chacun des deux éléments (Hg et Se) augmente quand ils sont administrés simultanément; (3) à la suite d'une période de contamination au mercure, le taux d'excrétion peut être augmenté par l'administration de sélénium dans la diète.

Le mécanisme le plus fréquemment cité propose la formation de complexes stables entre le mercure (Hg^{2+} et RHg^+) et une source protéique non enzymatique de sélénium présente sous les formes −SeH, −Se−Se−, ou −S−Se−S−. Ainsi, le mercure et le sélénium sont accumulés simultanément dans l'organisme, mais le mercure est rendu inoffensif, ne pouvant plus se lier aux groupes sulphydryles des protéines. Dans certains cas, les complexes peuvent ensuite être éliminés lentement par l'organisme (Magos et Webb 1980).

Chez *Mytilus edulis*, on peut résumer les observations en quatre points : (1) le sélénium accumulé ne réduit pas la toxicité du mercure (Hg^{2+} et CH_3Hg^+); (2) le mercure et le sélénium ne s'accumulent pas dans des proportions constantes; (3) le mercure augmente la rétention du sélénium mais le taux d'accumulation du mercure n'est pas modifié par le sélénium; (4) même quand CH_3Hg^+ cesse de s'accumuler, le sélénium inorganique continue à augmenter dans le tissu de la moule.

Le mécanisme décrit plus haut n'est pas applicable au cas de la moule. Ce mollusque ne semble pas posséder les mécanismes régulateurs des mammifères terrestres ou marins (Martoja et Martoja 1978) et n'est probablement pas en mesure de synthétiser les dérivés sélénoprotéiques nécessaires à la complexation Hg−Se. L'accumulation du sélénium observée dans notre expérience peut avoir été causée par un dérèglement métabolique dû à la présence d'un très grand excès de sélénium dans le milieu et à l'intoxication au mercure. La conjugaison de ces deux facteurs pourrait par exemple réduire la spécificité de certaines enzymes responsables de la synthèse des dérivés sulphydryles et entraîner l'assimilation du sélénium à la place du soufre. Le problème de la sélectivité du soufre et du sélénium a été longuement discuté par Shrift (1972) pour les plantes et les microorganismes et il pourrait probablement être présent chez d'autres organismes, surtout chez ceux qui sont soumis à un stress important. Il est aussi possible que l'effet toxique du mercure se fasse sentir au niveau des fonctions métaboliques de l'organisme et que l'élimination du sélénium soit bloquée par l'action du mercure et surtout du méthyl mercure. Cette hypothèse est soutenue par l'observation d'une latence à l'augmentation de la concentration en sélénium dans au moins deux cas (bassins 1 et 8B), ce qui indiquerait une certaine résistance de l'organisme à l'invasion du sélénium par une élimination adéquate jusqu'à ce que l'intoxication devienne trop marquée.

À la lumière des résultats obtenus, il apparaît certain que la notion d'antagonisme telle que décrite pour d'autres organismes ne s'applique pas au cas de *M. edulis*. On observe tout de même une interaction mercure−sélénium qui pourrait être liée à un dérèglement métabolique chez le mollusque.

Épuration

L'utilisation des dérivés sulphydryles comme agents complexants pour réduire la toxicité du mercure et/ou accroître son élimination a été mentionnée à plusieurs reprises (Rabenstein *et al.* 1983 et les nombreux travaux qui y sont cités). Dans le cas du sélénium, le problème a été abordé par Rudd *et al.* (1983) pour un écosystème d'eau douce. Il a été démontré que le sélénite de sodium pourrait être utile pour réduire la présence du mercure dans la biocénose. Dans le même ordre d'idées, on peut envisager la possibilité d'utiliser un dérivé organique ou minéral du sélénium pour accroître l'épuration *in vivo* d'organismes marins d'intérêt commercial qui auraient été contaminés par le mercure. Dans le cas de *M. edulis*, nos résultats montrent qu'il est peu probable que le sélénium puisse jouer un rôle quelconque sur le taux d'élimination du mercure.

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Ecological Significance of the Ctenophore *Pleurobrachia pileus* off Southwestern Nova Scotia

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The population dynamics and quantitative feeding ecology of the ctenophore (*Pleurobrachia pileus*) were investigated in the spring of 1983 and 1984 on Browns Bank, southwestern Scotian Shelf. In both years, large crustacean zooplankton (>1050 μm) were the dominant item in the diet of *Pleurobrachia* among all sizes captured (range = 5–21 mm diameter) averaging 70% by weight of the total prey consumed. The daily ration of *Pleurobrachia* was strongly size dependent increasing from 2.6 mg dry wt./d at a body size of 6 mm to 8.5 mg/d at 12 mm. At the population level, daily consumption of crustacean zooplankton during 1983 and 1984 averaged 8.8% (range = 0.2–28%) and 0.7% (range = 0.2–2%) of the prey standing stock, respectively. This difference was consistent with the observation that there was 28% less zooplankton, on average, during 1983 relative to 1984 at the same time and location. An abnormal spring peak in ctenophore abundance was evident in 1983, but not in 1984, that consisted of large, mature individuals at average densities in excess of $1/m^3$. Ctenophore abundance during spring of 1984 averaged $0.1/m^3$. Increased overwintering survival of ctenophores resulting from anomalously high sea surface temperatures (SST) appears to have been responsible for the exceptional spring abundance of *Pleurobrachia* on Browns Bank during 1983. Over 50% of the variation in a 10-yr time series of spring *Pleurobrachia* abundance for the southwest Nova Scotia region was explained by SST conditions prevailing during January to April. I suggest that the extremely low levels of haddock (*Melanogrammus aeglefinus*) larvae produced on Browns Bank during the spring of 1983 resulted from food shortages induced by severe depredation of zooplankton by *Pleurobrachia*.

Au printemps de 1983 et de 1984, on a étudié la dynamique de la population et l'écologie de l'alimentation quantitative du cténophore *Pleurobrachia pileus* sur le banc de Brown, au sud-ouest de la plate-forme Scotian. Les deux années, du zooplancton constitué de gros crustacés (>1050 μm) était l'élément principal du régime alimentaire des individus de toutes tailles capturés (diamètre variant de 5 à 21 mm), représentant en moyenne 70 % du poids de toutes les proies consommées. La ration quotidienne de *Pleurobrachia* dépendait beaucoup de la taille, passant de 2,6 mg de poids sec/jour pour une taille de 6 mm à 8,5 mg/jour pour une taille de 12 mm. Au niveau de la population, la consommation quotidienne de crustacés zooplanctoniques en 1983 et 1984 a représenté en moyenne respectivement 8,8 % (échelle de 0,2 à 28 %) et 0,7 % (échelle de 0,2 à 2 %) de la biomasse des proies. Cette différence était en accord avec l'observation qu'il y avait en moyenne 28 % moins de zooplancton en 1983 qu'en 1984 à la même époque et au même endroit. Un nombre maximal anormal de cténophores a été observé au printemps de 1983 mais pas en 1984 : il s'agissait de gros individus adultes, dont la densité moyenne dépassait $1/m^3$. Au printemps de 1984, le nombre de cténophores se chiffrait en moyenne à $0,1/m^3$. Une survie accrue de cténophores pendant l'hiver, attribuable à des températures de la mer anormalement élevées en surface (TMS), semble avoir été à l'origine de l'abondance exceptionnelle de *Pleurobrachia* au printemps sur le banc de Brown en 1983. Plus de 50 % des écarts d'une série chronologique de données étalée sur 10 ans sur l'abondance au printemps de *Pleurobrachia* dans la région du sud-ouest de la Nouvelle-Écosse ont été expliqués par les conditions existantes de TMS de janvier à avril. J'émets l'hypothèse que les quantités extrêmement faibles de larves d'aiglefin (*Melanogrammus aeglefinus*) produites sur le banc de Brown au printemps de 1983 sont attribuables au manque de nourriture provoqué par une déprédation intense de zooplancton par *Pleurobrachia*.

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Fraser (1970) was among the first to recognize the ecological significance of ctenophores in the pelagic food web, suggesting that they act as serious competitors for crustacean zooplankton with pelagic fish and the planktonic larval stages of most fish. What is currently known about the feeding ecology and population dynamics of ctenophores has been derived from studies conducted in coastal embayments, estuaries, and mesocosms (see reviews in Fraser 1970; Reeve and Walter 1978; Alldredge 1984). Collectively, these studies show that ctenophores exhibit high ingestion rates at high food densities, periodic decimation of prey standing stocks is common where ctenophores are locally abundant, and variable seasonal and interannual levels of abundance frequently result owing to their remarkable capacity to rapidly exploit favorable environmental conditions. Temporal variability in ctenophore abundance at seasonal time scales and longer, coupled with their enormous feeding potential at bloom levels ($>1/m^3$), makes prediction of their impact on prey and

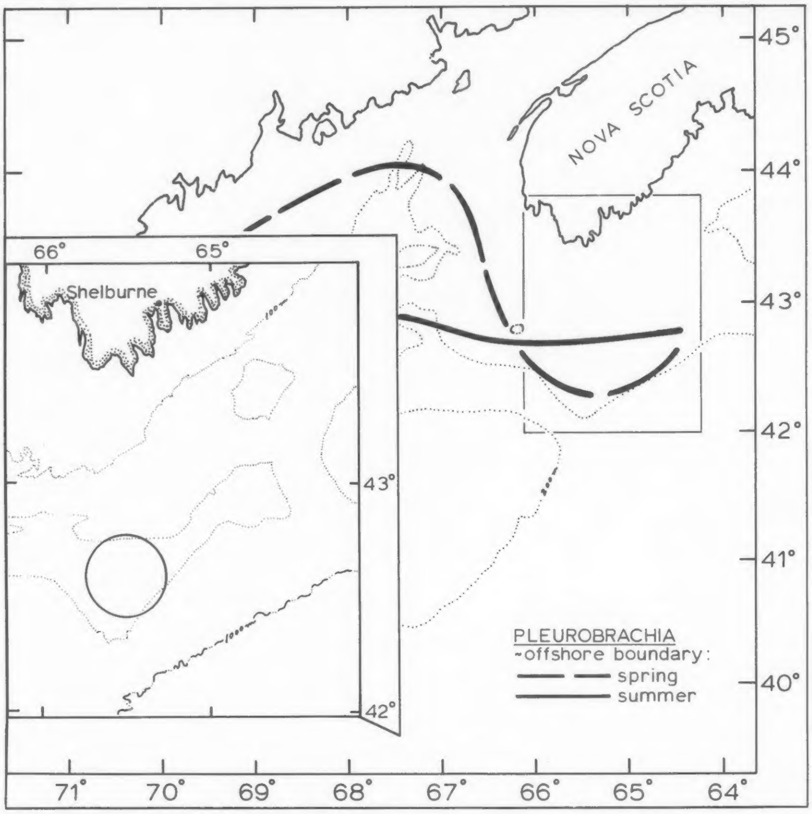

FIG. 1. Shelf region off southwestern Nova Scotia and the approximate spring and summer southern offshore boundary of *Pleurobrachia pileus* in the Gulf of Maine – Browns Bank region (after Bigelow 1926). Inset shows location on Browns Bank where intensive plankton sampling was conducted (area enclosed by circle) during May, July, and November in 1983 and 1984.

competitor species difficult at best. Under these circumstances it would be incorrect to assign ctenophores to a permanent ecological role in a pelagic food web.

Studies on the ecology of ctenophores in the offshore continental shelf waters are surprisingly few (Bigelow 1926; Fraser 1970; Tungate 1975) although these waters are centers of intense spawning activity that serve as nursery zones for the offspring of many commercially important fish and shellfish (Colton et al. 1979; Grosslein and Azarovitz 1982; Scott 1983; O'Boyle et al. 1984). Indirect consideration has been given to the quantitative significance of ctenophores in shelf ecosystems through a trophic production model for the Scotia Shelf (Mills and Fournier 1979; Mills 1980) and a simulation model of Georges Bank (Davis 1984). Both approaches suggest that ctenophores might be an important component controlling energy flow in shelf waters.

The community structure of the Scotian Shelf ecosystem, in particular, is not generally agreed upon. In fact, alternative models relying heavily on field measurements of abundance and the turnover rates of the component populations (Sameoto 1982; Tremblay and Roff 1983; Sinclair et al. 1984) do not support the hypothesis of a food chain dominated by ctenophores. However, disparities exist in the sample data base for ctenophore abundance on the shelf ranging from seldom collected (Sameoto 1982), abundant in spring months (Bigelow 1926), to abundant at some locations in the fall (Tremblay 1981). The population attributes of ctenophores known from coastal studies combined with limited, nontargeted sampling effort in the offshore has resulted in the absence of any direct estimate of the quantitative significance of ctenophores on the Scotian Shelf. The study by Sameoto (1982) illustrates this problem: plankton samples collected in May 1977, June 1978, and April 1979 on the Scotian Shelf yielded few ctenophores. The conclusion drawn from this inappropriate sampling strategy for ctenophores, i.e. that ctenophores were seldom a significant component of the ecosystem, is likely premature. Single sample surveys of communities do not provide accurate statements of the structuring of communities, and equilibrium conditions are highly improbable (Wiens 1981). Extensive temporal sampling within a year or during the same season and location between years is a prerequisite for effective evaluation of ctenophore abundance.

I investigated the population dynamics and quantitative feeding ecology of the ctenophore *Pleurobrachia pileus* on the Scotian Shelf. The object of the study was to resolve the uncertain ecological status of this species in the offshore pelagic food web. A deliberate decision was made to examine the spring time period of Browns Bank in detail. Here, late-winter and spring spawning of commercial stocks of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) is known to occur

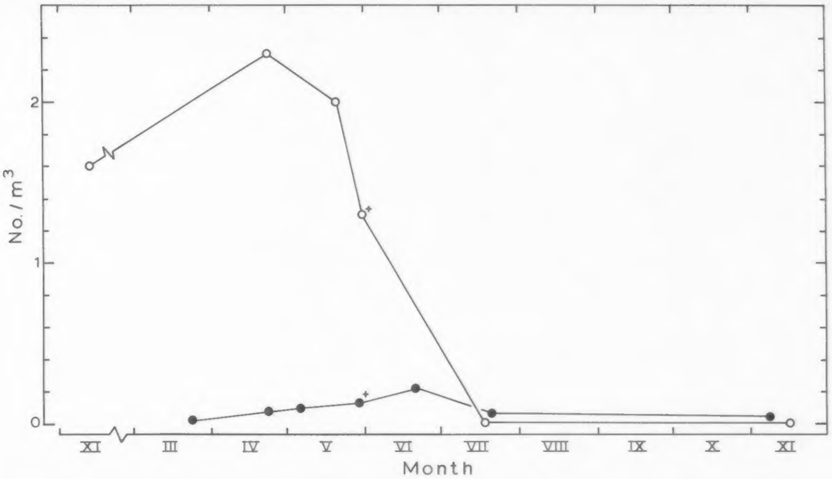

FIG. 2. Seasonal mean abundance of *Pleurobrachia* in the Browns Bank region during 1983 (○) and 1984 (●). A plus sign indicates time period during which interannual comparison of ctenophore consumption was made.

(Scott 1983; O'Boyle et al. 1984). *Pleurobrachia pileus* is also known to reside in the area (Bigelow 1926; Fig. 1). This sampling plan made possible the testing of the food competition hypothesis of Fraser (1970): swarms of *Pleurobrachia* deplete stocks of zooplankton leading to food shortages for fish larvae and, eventually, increased larval mortality.

Materials and Methods

The study site, Browns Bank, is located on the southwestern end of the Scotian Shelf approximately 100 km south of Shelburne, Nova Scotia (Fig. 1). Thirteen equally spaced stations were established for intensive plankton sampling during 1983 and 1984 over the eastern saddle of the bank bounded by the following coordinates: 42°45.0′N, 42°25.0′N; 65°44.0′W, 65°16.0′W. The eastern saddle of the bank is characterized by monotonous bathymetry (depth range 90−100 m) and relatively weak residual barotropic currents (1−3 cm/s) generated by tides and steady winds (Greenberg 1983). It is less physically dynamic than the shallower western cap of Browns Bank. A permanent anticyclonic gyre typifies the larger scale circulation pattern of the bank (Smith 1983). In 1983, I sampled the grid during 23−30 May, 12−16 July, and 14−21 November, and in 1984 during 2−8 May, 22−29 May, 16−22 July, and 1−7 November. Research cruises to Browns Bank were also conducted during 21−25 February and 21−25 April 1983 (reported by Dugas 1984) and 20−27 March, 20−24 April, and 15−20 June 1984 (Marine Fish Division, Scotia−Fundy Region). Collectively, these cruises provided data on ctenophore abundance in the region.

I obtained depth-integrated plankton samples of the mixed layer with oblique tows using two 61-cm-diameter, 333-μm-mesh nets attached to an aluminum bongo frame fitted with a T.S. flowmeter (Tsurumi-Seiki Co., Ltd.). An electronic temperature/depth sensor contained in a towed body was attached approximately 0.5 m above the bongo frame. The base of the mixed layer was detected by observing the onboard graphic display of the temperature/depth signal on an $X-Y$ plotter. Sampling of the mixed layer with bongo gear was conducted during all of my cruises to the bank in 1983 and only during the 22−29 May 1984 cruise. Sampling depths generally ranged between 20 and 30 m. Towing times averaged 10 min and towing speeds were, on average, 1.5 m/s. The time between sample collections was approximately 2−3 h.

I determined the vertical distribution of ctenophores and their potential prey from discrete depth sampling conducted during 1984 using a small-scale version of the BIONESS (Sameoto et al. 1980). The gear is capable of sampling up to seven discrete depths on command via an electrical signal transmitted along the conducting towing cable. The mouth area of each 333-μm-mesh net was 0.25 m^2 and towing speeds generally averaged 1.5 m/s. One electronic flowmeter (modified T.S.) positioned in the mouth of the net and one attached to the outside frame provided estimates of flow rate and filtration efficiency. An Applied Microsystems CTD positioned on top of the net frame provided real-time estimates of temperature, salinity, and depth. All electronically monitored data was displayed on a video screen of a dedicated microcomputer (Commodore Pet) and transferred directly to disk for storage. Sample depths were 5, 10, 20, 35, 45, 55, and 65 m. Each depth stratum was sampled for a 10-min period. The time interval between consecutive stations averaged 3−4 h. The vertical distribution of ctenophores and their potential prey are reported from the 2−8 May 1984 cruise. Data on ctenophore vertical distribution are also shown from the 16−22 July 1984 cruise.

On deck, all plankton samples, irrespective of the gear type used, were treated identically. Initially, the contents of each cod end were passed through a 4-mm-mesh sieve to remove ctenophores. Ctenophores and the remainder of the sample were placed into separate containers and preserved in a 5% buffered formalin and seawater solution. Ctenophores were individually counted and measured to the nearest 1.0 mm by determining the linear distance from the oral to aboral pole (= polar diameter). Ichthyoplankton were identified to species and counted. Ichthyoplankton and ctenophore abundance were expressed as number per cubic metre.

The balance of the plankton sample (that passing through the 4-mm-mesh sieve), the bulk of which was copepods, was fractionated into four size categories, 308−602, 602−860, 860−1050, and >1050 μm, by washing through a graded series of sieves stacked from largest (1050 μm) to smallest (308 μm). This fractionation procedure was intended to provide a better measure of prey availability to the various sizes of fish larvae and ctenophores than total biomass estimates alone. The four fractions were rinsed with freshwater, resuspended, and filtered by aspiration through a preweighed glass microfiber filter. The filters were placed in a drying oven at 70°C for 24 h, removed to a desiccator, and weighed to an accuracy of 10 μg. The dry weight biomass of each size fraction was determined by difference. All dry weight determinations were expressed as milligrams per cubic metre. Data derived in this manner are presented for the 1983 and 1984 May cruises.

The dominant ctenophore species collected during the cruises in both years was *P. pileus*. The diet of this species was determined solely for the 1983 and 1984 May cruises. A maximum of 25 individuals selected at random from each station were examined for stomach contents. When less than 25 occurred in the sample, all individuals in the sample were analyzed. Prior to each dissection, ctenophore body size was measured. All prey items were identified and counted from each excised pharynx. Following this procedure all prey items from ctenophores captured during each cruise were pooled. This prey conglomerate was fractionated by size and dry weights were determined in the same manner used to evaluate the at large crustacean zooplankton biomass. The number of particles retained by each sieve was counted to determine the average weight per particle within each of the four size categories.

Ctenophore and ichthyoplankton densities and the dry weight biomass of zooplankton from the four size categories were ln $(Y + 1)$ transformed prior to correlation analysis because the untransformed data exhibited a tendency for the variance to be positively correlated to the mean. This transformation effectively stabilized the variance.

Results and Discussion

Seasonal Abundance

Pronounced differences in the timing of the seasonal peak in *Pleurobrachia* abundance was evident between 1983 and 1984 over Browns Bank. In 1983, ctenophore density was maximum during late April (average = $2/\mathrm{m}^3$) with high levels of abundance persisting into late May (average = $1/\mathrm{m}^3$; Fig. 2). The density of *Pleurobrachia* witnessed during the spring of 1983 was equivalent to "blooms" or outbreaks that typically occur in this region during the summer months (Sherman et al. 1979; Milne 1984). The abnormal appearance of large numbers of ctenophores during the spring months contrasted strongly with virtual absence from the region in July when they are typically abundant (Sherman et al. 1979; Milne 1984). Temporal changes in *Pleurobrachia* abundance during 1984 were much closer to the expected pattern (Fig. 2). Ctenophore abundance during late May 1984 was significantly lower (mean = $0.1/\mathrm{m}^3$; $t = 3.03$, $P < 0.01$, df = 31) than the level of abundance measured at the same time and location in 1983 (Fig. 2). The maximum 1984 abundance, recorded during the month of June, was extremely low (mean = $0.2/\mathrm{m}^3$). The only similarity in the seasonal pattern of *Pleurobrachia* abundance between years occurred in November when ctenophores were absent from the bank waters.

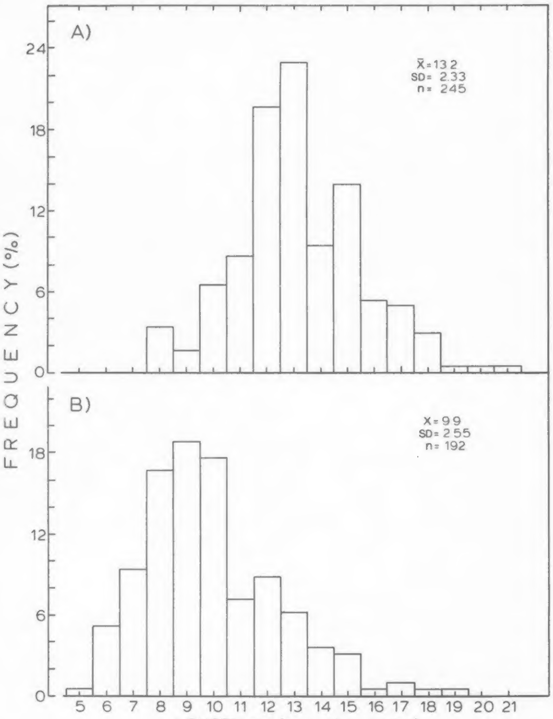

FIG. 3. Size frequency distribution of *Pleurobrachia* population during late May of (A) 1983 and (B) 1984.

Size Composition and Growth

The size frequency distribution of *Pleurobrachia* differed significantly in late May of 1983 and 1984 (Kolmogorov−Smirnov test, $D_{\max} = 0.569$, $P < 0.001$; Fig. 3). The spring collections made in 1983 contained, on average, larger specimens (13.2 mm in diameter, range = 8−21 mm) than those captured at the same time and location in 1984 (9.9 mm in diameter, range = 5−19 mm). Small, immature *Pleurobrachia* (<6 mm in diameter; Greve 1970) normally dominate during periods of maximum abundance (Fraser 1970; Yip 1981; van der Veer and Sadee 1984; Milne 1984), indicating that the great abundance of large, mature *Pleurobrachia* present during the spring of 1983 deviated considerably from the expected pattern. Fraser (1970) hypothesized that a similar situation in the North Sea resulted from increased survival over the previous winter. Ctenophores that appear during the spring months have typically overwintered as juveniles and thus are products of the previous year's spawning (Bigelow 1926; Fraser 1970 and references contained therein; Milne 1984). The observation that *Pleurobrachia* was very abundant (average density $>1/\mathrm{m}^3$) in the southwest Nova Scotia region prior to the onset of the 1982−83 winter season (Fig. 2; Milne 1984) supports the overwintering survival hypothesis. Seasonal body size data were unavailable for the remaining cruises conducted during 1983 (Dugas 1984).

During 1984, body size data were collected on five of seven cruises. Ctenophore body size averaged 3.8 mm in March, 6.0 mm in April, 7.7 mm in early May, and 9.9 mm in late May. *Pleurobrachia* growth rates (calculated from the differ-

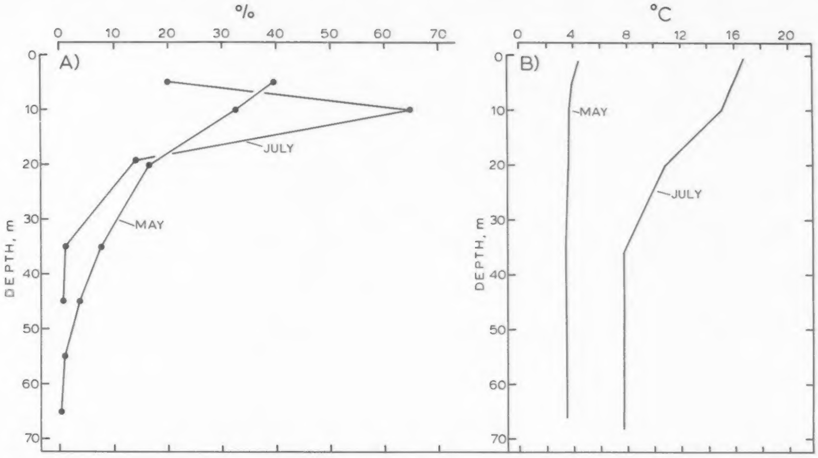

FIG. 4. (A) Depth distribution of *Pleurobrachia* during early May and July of 1984; values are the percentage of ctenophores at a given depth relative to their total abundance over the entire water column. (B) Temperature vs. depth profile corresponding to Fig. 4A.

ence in average body size between consecutive cruises and the elapsed time) increased from 0.07 to 0.12 mm/d during the late winter to spring period and appeared to parallel changes in surface water temperature, which rose from 3 to 6.5°C over the period. The growth rates estimated for *Pleurobrachia* during this period are entirely consistent with the growth rate of 0.10 mm/d reported by Greve (1972) for *Pleurobrachia* grown under optimal experimental conditions at 6°C. The similarity between field and laboratory derived growth rate estimates signifies continuity of the population of *Pleurobrachia* sampled on Browns Bank. Very few large *Pleurobrachia* were collected during July although increased numbers of small individuals (mean = 6.4 mm, range = 1–11 mm) were evident, indicating that spawning and hatching had occurred. This observation agrees with the expected size composition of *Pleurobrachia* for the summer months in the southwest Nova Scotia region (Milne 1984).

Vertical Distribution

Eighty-eight percent of the *Pleurobrachia* collected over the bank in early May of 1984 occurred in the upper 20 m of the water column when temperature conditions were virtually isothermal with depth (Fig. 4). In July the bank waters were well stratified and 98% of the population, albeit low in abundance, occurred in the upper 20 m of the water column. The consistent near-surface vertical distribution of *Pleurobrachia* under isothermal (May) and thermally stratified (July) conditions on the bank suggests that the surface waters are the preferred depth zone for this species. Bigelow (1926) and Anderson (1974) both found *Pleurobrachia* to reside in the upper 30 m of the water column in Nova Scotian waters and that this depth distribution remained unchanged with time of day. Similar findings have been reported from other geographic regions (Hirota 1974; Yip 1981).

Feeding Ecology

The diet of *Pleurobrachia* during the spring period of study was dominated by crustacean zooplankton >1050 μm, averaging 70% (dry weight) of the total prey consumed. The proportion of large zooplankton (principally calanoid copepods) in the diet remained unchanged in spite of the wide variation in size of ctenophores (range of means for each sampling period = 7.7–13.2 mm) collected during May in 1983 and 1984 (Fig. 5). The close resemblance of the percent size composition of prey in the diet relative to their availability in the field, which was quite similar during the three study periods (Fig. 5), indicates a nonselective, density-dependent pattern of prey exploitation by *Pleurobrachia*. In absolute terms, the bio-

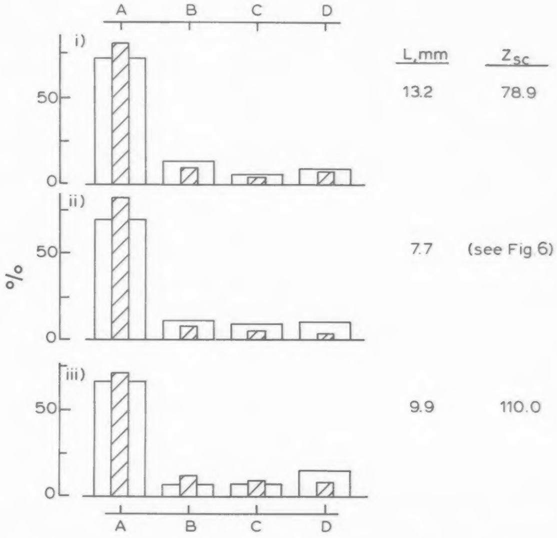

FIG. 5. Percent composition of four size categories of crustacean zooplankton at large (hatched bars) and in the diet of *Pleurobrachia* (open bars). Zooplankton size categories: A, >1050 μm; B, 860–1050 μm; C, 602–860 μm; D, 308–602 μm; *L*, mm refers to average ctenophore body size; Z_{sc} is the average standing crop of crustacean zooplankton (mg dry weight/m^3) for all size fractions during cruise periods (i) 23–30 May 1983, (ii) 2–8 May 1984, and (iii) 22–29 May 1984.

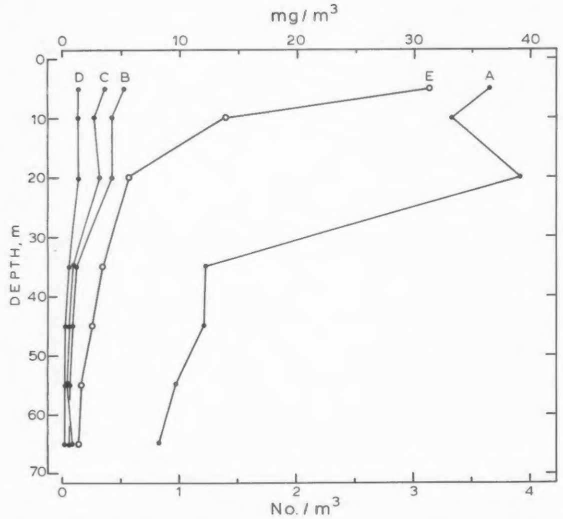

FIG. 6. Depth distribution of crustacean zooplankton (●) and fish eggs (○) during early May of 1984. Four dry weight biomass size categories of zooplankton are shown (A, >1050 μm; B, 860–1050 μm; C, 602–860 μm; D, 308–602 μm); E refers to fish eggs expressed as no./m^3.

mass of the at large crustacean zooplankton >1050 μm was sevenfold greater than the other size categories. There were only slight differences among the three smaller size groups. Fish eggs and *Oikopleura* sp. were found in less than 2% of the stomachs examined ($n = 600$) and fish larvae were completely absent. Crustacean zooplankton have generally been shown to be the major prey of *Pleurobrachia* (Fraser 1970; Anderson 1974; Milne 1984). Laboratory studies (Grice et al. 1980; Stanlaw et al. 1980) have shown that *Pleurobrachia* ingest the largest potential prey available after attaining a body size >1 mm, with copepodites and adult copepods providing the bulk of their carbon intake. Hirota (1972) found that the optimal ratio (for successful growth) of prey particle size to *Pleurobrachia* body size (equatorial diameter, millimetres) was 0.2–0.3 (note: equatorial diameter ≃ 0.80 polar diameter).

The vertical distribution of crustacean zooplankton shows both the dominance of zooplankton >1050 μm over the other size groups at all sample depths and the concentration of this large size fraction in the upper 30 m of the water column (>80%; Fig. 6). The strongly overlapping vertical distribution of *Pleurobrachia* with the center of abundance of its principal prey was not unexpected; however, the virtual absence of fish eggs in the ctenophore diet given their high concentration (>3/m^3) in the surface layer (>85% in the upper 20 m) was unexpected.

There was no periodicity in the feeding incidence (number of ctenophores at a station with recognizable prey in the gut per total number of guts examined) of *Pleurobrachia*. This conclusion was based on the lack of significant linear and polynomial regressions ($P > 0.05$) obtained from the analysis of feeding incidence and time of day for each of the 1983 and 1984 May cruises. *Pleurobrachia* has been previously shown to exhibit a uniform feeding rate throughout the day (Anderson 1974; Milne 1984). The feeding incidence recorded during May of 1983 was the lowest observed, averaging 46% (95% confidence interval = 36–56%). The maximum level was found during late May of 1984 when 84% of the population, on average, was feeding (95% confidence interval = 76–92%). An intermediate average value of 55% (95% confidence interval = 45–65%) was obtained from the early May period of 1984. The feeding incidence measured during the two late May sampling periods between years tended to parallel the quantity of total zooplankton biomass available to the ctenophores.

Over the upper four depth strata sampled (5, 10, 20, and 35 m) during early May 1984, feeding incidence was directly related to the concentration of zooplankton >1050 μm ($r = 0.95$, $P < 0.05$). Feeding incidence over the total number of depths sampled was as follows:

Depth (m)	5	10	20	35	45	55	65
% feeding	51.5	53.4	61.8	35.5	55.2	44.4	—

The amount of prey taken per ctenophore was also independent of time, although the discrete depth sampling revealed a twofold greater number of prey per gut, on average, among ctenophores collected in the upper 20 m relative to those few individuals (12% of the total abundance) found below this depth (five prey per gut versus two).

Daily Consumption

The weighted average dry weight ($\bar{w}$) of an individual prey particle, calculated from the equation

$$(1) \quad \bar{w} = \sum_{i=1}^{4} p_i w_i$$

where p_i is the proportion of the diet composed of prey in the ith size category (Fig. 5) and w_i is the average weight (milligrams) of a prey particle in the ith size class, was quite similar among the 1983 and 1984 May sampling periods, ranging from 0.108 to 0.111 mg. The product of $\bar{w}$ and the number of prey per ctenophore, averaged over each 1-mm body size interval from 5 to 21 mm, exhibited a significant positive relationship with ctenophore body size. An equation describing this relationship is

$$(2) \quad Y_{A_i} = 0.0927X_i - 0.3137, \quad r = 0.67, n = 31, P < 0.01$$

where X_i is the polar diameter (millimetres) of *Pleurobrachia* in the ith size class and Y_{A_i} is the average dry weight (milligrams) of prey in the gut of an individual in the ith size class. There was no significant difference in the average quantity of prey per gut among similar size ctenophores from the 1983 and 1984 May sampling periods. The maximum gut capacity of ctenophores within each size class was also evaluated by regressing Y_{M_i} (defined as the product of the maximum number of prey per ctenophore in each size class and $\bar{w}$) against ctenophore body size (X). This yielded the equation

$$(3) \quad Y_{M_i} = 0.1865X_i - 0.095, \qquad r = 0.68, n = 31, P < 0.01.$$

A digestion time of 2.26 h has been estimated for *Pleurobrachia* feeding on copepods in St. Margaret's Bay, N.S., at water temperatures ranging between 3.5 and 5°C (Anderson 1974). Both the food source and temperatures are equivalent to the conditions commonly experienced by *Pleurobrachia* during May on the bank. This indicates that the digestion time can be used with confidence to establish a daily ration.

Daily ration was defined as

$$(4) \quad R_i = (Y_{A_i} \cdot D^{-1} \cdot 24 \text{ h})$$

TABLE 1. Summary of parameter values used in eq. 2−6 to estimate daily removal of crustacean zooplankton by *Pleurobrachia* inhabiting Browns Bank. Means and ranges were derived from interstation estimates. Symbols are defined in text.

	N	Body size (mm)	F	Z_{sc}	M	
					Avg.[a]	Max.[b]
1983						
Mean	1.29	13.2	0.46	78.9	8.8	23.4
Range	0.05−3.91	7.8−15.0	0.16−1.00	30.8−147.8	0.2−28.4	0.5−73.4
1984						
Mean	0.12	9.9	0.84	110.04	0.7	2.1
Range	0.02−0.40	9.0−12.6	0.69−1.00	35.1−177.2	0.2−1.9	0.7−5.7

[a] Based on eq. 2.
[b] Based on eq. 3.

where R_i = daily ration (milligrams dry weight) of a ctenophore in the ith size class, Y_{A_i} is the average gut content of a ctenophore in the ith size class, and D is digestion time = 2.26 h. The maximum daily ration was calculted by replacing Y_A with Y_M in eq. 4. The major assumptions underlying the development and application of eq. 4 include (i) the absence of any significant net feeding by ctenophores, addressed and dismissed as nonsignificant by Anderson (1974) and Hirota (1974), (ii) digestion rate is independent of ctenophore body size, shown to be valid for *Pleurobrachia* by Harris et al. (1982), and (iii) ctenophores feed continuously during day and night and the feeding rate is paralleled by the rate of digestion, supported by the absence of any clearly defined periodicity in feeding incidence shown in this study and others, and the lack of evidence that ctenophores consume individual prey particles large enough to satisfy their daily energy requirements. The average weight of prey consumed daily by *Pleurobrachia* 8, 10, and 13 mm in polar diameter (based on approximate average sizes from the three May sampling periods in May; Fig. 5), calculated from eq. 4, equates to 20, 29, and 43 adult *Calanus finmarchicus* females, respectively (average weight of an individual female = 0.222 mg dry weight, n = 150, G. Harding, Marine Ecology Laboratory, Bedford Institute of Oceanography, unpubl. data). Maximum daily consumption is approximately threefold greater. These estimates are similar to the values reported by Bishop (1968) and Reeve et al. (1978) for *Pleurobrachia* (6−10 mm in diameter) feeding on natural copepod assemblages. Expression of daily ration as a *Calanus* equivalent stems from the observation that adult *Calanus* is an important prey item of North Sea ctenophores, particularly during January to May when they occasionally represent >50% (by numbers) of the total prey consumed (Fraser 1970). Also, during spring on the Scotian Shelf, *Calanus* comprises 90% of the total Copepoda (Sameoto 1982).

Prey consumption by *Pleurobrachia* at the population level was determined by adjusting the daily ration (R) for feeding incidence (F) and ctenophore density (N) using the equation

$$(5) \quad C = R \cdot F \cdot N$$

where C = daily quantity of prey consumed (milligrams dry weight per cubic metre) and N = number of ctenophores per cubic metre. Equation 5 was evaluated for both the average and maximum size-specific daily ration. The total proportion of the zooplankton standing stock consumed on a daily basis was estimated as

$$(6) \quad M = (C/Z_{sc}) \cdot 100$$

where M = prey removal rate (percent per day per cubic metre), C = daily consumption of prey (milligrams dry weight per cubic metre), and Z_{sc} = zooplankton standing stock (milligrams dry weight per cubic metre).

The daily consumption of zooplankton by *Pleurobrachia* over the bank during late May of 1983 and 1984 averaged 8.8% (range = 0.2 − 28%) and 0.7% (range = 0.2 − 2%) of the zooplankton standing stock, respectively (Table 1). The maximum daily consumption was, on average, 23 and 2% of the prey standing stock for 1983 and 1984, respectively (Table 1). The daily predation rate estimated for *Pleurobrachia* during late May of 1983 was compared with the reduction in total copepod density (less nauplii) measured by Dugas (1984) during two sampling periods (8−9 May and 20−27 May 1983) on the eastern cap of Browns Bank. During the 15-d period separating the two cruises, copepod abundance declined from 9349 to 2151 individuals/m^3, yielding an instantaneous mortality rate of 9.8%/d. The similarity between this value and the model prediction suggests that the model may be a realistic estimator of the predation effect by *Pleurobrachia*. This comparison assumes, of course, that ctenophore predation was the major source of copepod mortality during this time period and that the copepod density estimates reflect the true abundance in the region.

Interstation variability in zooplankton biomass due to ctenophore predation was predicted a priori to be most evident *only* during May 1983 and *only* within the zooplankton size category >1050 μm. The existence of significant inverse correlations between ctenophore abundance and zooplankton biomass (Table 2) supports the prediction. All correlation coefficients were nonsignificant for May 1984, which suggests that predation pressure by *Pleurobrachia* was minimal at that time. The very different predation intensity evident between years might also explain, in part, the 28% lesser amount of total zooplankton measured in May of 1983 relative to 1984. The biomass of zooplankton in the 308−602, 602−860, and 860−1050 μm size categories during 1983 was also significantly lower (t-test, $P < 0.05$) than levels measured for 1984 at the same time and location (Table 2). Although these sizes are not preyed upon directly by *Pleurobrachia* (Fig. 5), their levels depend on reproduction by the individuals contained in the >1050 μm size category. Egg production rates of *C. finmarchicus* measured on Browns Bank in May of 1983 ranged from 20 to 30 eggs·female^{-1}·d^{-1} (Runge 1985). The equivalent average daily consumption of adult *C. finmarchicus* by *Pleurobrachia*

TABLE 2. (A) Correlations of ln *Pleurobrachia* density (no/m^3) and ln zooplankton biomass (mg dry wt./m^3) for each of four size categories of crustacean zooplankton and their combined abundance during late May of 1983 and 1984. (B) Interannual comparison of average zooplankton biomass for the four size categories of crustacean zooplankton and total abundance. Comparisons based on t-test under the assumption of equal variances. $^*P < 0.05$; $^{**}P < 0.01$.

		Zooplankton size fraction (μm)				
	Year	308−602	602−860	860−1050	>1050	Total biomass
A	1983	0.30	0.04	−0.37	−0.54*	−0.43*
	1984	0.15	0.37	0.37	0.56	0.48
B	1983	4.86	2.94	7.10	64.01	78.91
	1984	9.57	10.41	12.22	77.84	110.04
	% difference	50	72	42	18	28
	t	3.26**	3.21**	2.04*	1.02	1.91

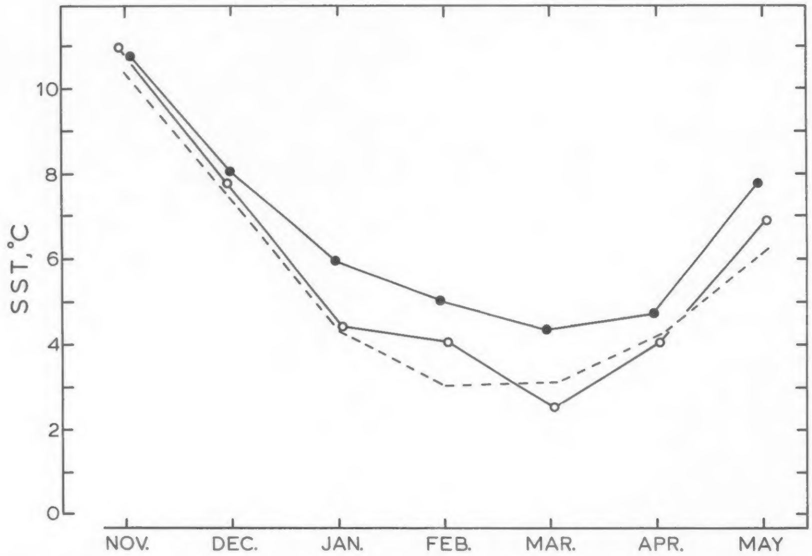

FIG. 7. Monthly mean sea surface temperatures for the Browns Bank region from November to May 1982−83 (●) and 1983−84 (○). Dashed line shows long term average (1972-1980) derived from same region.

at this time would have the effect of eliminating 1000 copepod eggs·d^{-1}·ctenophore 13 mm in polar diameter^{-1}. Such an effect could act to limit the food available to first-feeding cod and haddock larvae that are known to feed exclusively on copepod eggs and nauplii (Marak 1960; Kane 1984).

Ichthyoplankton−Ctenophore Interactions

The extremely variable predation pressure exerted by *Pleurobrachia* and its corresponding effect on crustacean zooplankton biomass was not parallel by changes in fish egg density. Egg densities, greater than 80% of which were identified as cod and haddock, were similar between years during the late May period, averaging 0.8/m^3 (maximum = 2.0/m^3) in 1983 and 1.3/m^3 (maximum = 2.6/m^3) in 1984. The observed low frequency of occurrence of fish eggs in the diet of *Pleurobrachia* (this study; Fraser 1970; Hirota 1974) may not indicate a lack of predation because it has been argued that rapid digestion of fish eggs and larvae precludes any quantitative evaluation of their importance in a predator's diet (Hunter 1984). However, the observation that fish egg density and *Pleurobrachia* abundance was strongly positively correlated during late May in 1983 and 1984 yielding $r = 0.87$ ($P < 0.001$) and $r = 0.66$ ($P < 0.05$), respectively, suggests that fish eggs are largely unaffected by the overlapping presence of ctenophores. The immunity that fish eggs exhibit to predation by *Pleurobrachia* is certainly not related to their size, since cod and haddock eggs range in size from 1.3 to 1.5 mm in diameter which falls within the crustacean size range most commonly ingested by *Pleurobrachia* (Fig. 5). The most plausible explanation for the absence of eggs from the diet was in the feeding behavior of *Pleurobrachia*. Prey capture involves the extension of two lateral retractile tentancles in a web-like configuration while remaining stationary in the water column. For this reason, *Pleurobrachia* have been designated as "ambush" predators (Greve 1970; Anderson 1974) and rely on the swimming velocity of prey to effect captures. Also, in situ observations of feeding shows that jerking movements by the prey, once entagled in the tentacles, triggers the feeding response (Greve 1970). The characteristics that determine susceptibility of a potential prey item to predation by *Pleurobrachia* are not applicable to a motionless fish egg. Gamble (1977) reported that the lobate ctenophore *Bolinopsis infundibulum* ingested plaice (*Pleuronectes platessa*) eggs but ejected them from the gut in an undigested state after a few hours. These findings suggest that egg predation by ctenophores is, in general, an insignificant source of mortality to fish eggs.

Haddock and, to a lesser extent, cod are fish species whose reproductive success would most likely be affected by an early bloom of ctenophores on Browns Bank. The peak period of reproduction in haddock over the bank occurs in April and May. Cod spawning extends from January to May over a much broader geographic region (O'Boyle et al. 1984). Similar spawning patterns for these two species exist on Georges Bank, which led Sherman et al. (1984) to suggest that the narrow temporal and spatial spawning period of haddock would increase the vulnerability of their offspring to cohabiting predators. The wide annual fluctuation in haddock recruitment relative to cod was taken as support for this view (Sherman et al. 1984). Although the restricted sampling area investigated in this study precludes an adequate evaluation of the relative abundance or survival rate of haddock larvae on the bank at large, concurrent studies in the region allow for some informed comment. Extremely low levels of haddock larvae, one to two orders of magnitude lower than in recent years, were evident during eight cruises (extending from February to June) to the Browns Bank region in 1983. This led Koslow et al. (1985) to conclude that the 1983 haddock year-class was a failure. There appeared to have been a heightened but unexplained source of mortality associated with the immediate posthatching period causing this low level of larval haddock production.

One hypothesis to explain the apparent low level of recruitment for the 1983 haddock year-class is that the larval stages of haddock experienced food shortages resulting from severe depredation of crustacean zooplankton by *Pleurobrachia*. If low levels of haddock recruitment are actually linked to the abnormally high densities of spring *Pleurobrachia*, then there would be considerable utility in a model that predicted such an event. Both the seasonal abundance and size composition of the resident ctenophore population on Browns Bank were sufficiently different between 1983 and 1984 and so similar to a situation described by Fraser (1970) in the North Sea that his interpretation serves as the starting point for my analysis.

Briefly, Fraser (1970) attributed an abnormal spring peak in the abundance of *Pleurobrachia* in the North Sea to a positive temperature anomaly of 0.2°C from November to May in the northwestern North Sea. He suggested that increased overwintering survival was responsible for the early peak in abundance. The possibility that hydrographic conditions during the overwintering period are linked to the spring abundance of *Pleurobrachia* was tested using data collected in this study and the longer-term data series available for the region contained in Milne (1984).

Because *Pleurobrachia* is a resident of the surface water layer (Fig. 4), sea surface temperatures (SST) may be a useful indicator of the local oceanographic climate they experience. Monthly SST data for the Browns Bank region (42.0−43.0°N, 65.0−67.0°W) were examined from November to May, 1982−84, relative to the long-term monthly averages (1972−80) calculated for the region (Trites and Drinkwater 1985a, 1985b). The relevant features of this data series were (1) the 1983 monthly means exceeded the long-term average values by 1.4°C, on average, from January to May, (2) maximum positive anomalies of nearly 2°C occurred during the winter months of January and February of 1983, and (3) the monthly means for 1984 were all very close to normal (Fig. 7). These patterns in turn appear to be reflected in the *Pleurobrachia* population responses observed during the spring of 1983 and 1984 (Fig. 2) and would appear to support the overwintering survival hypothesis of Fraser (1970). Although the 1983 January to May SST's were anomalously high, they were all well within the range for normal haddock egg and larval development (Laurence 1974, 1978).

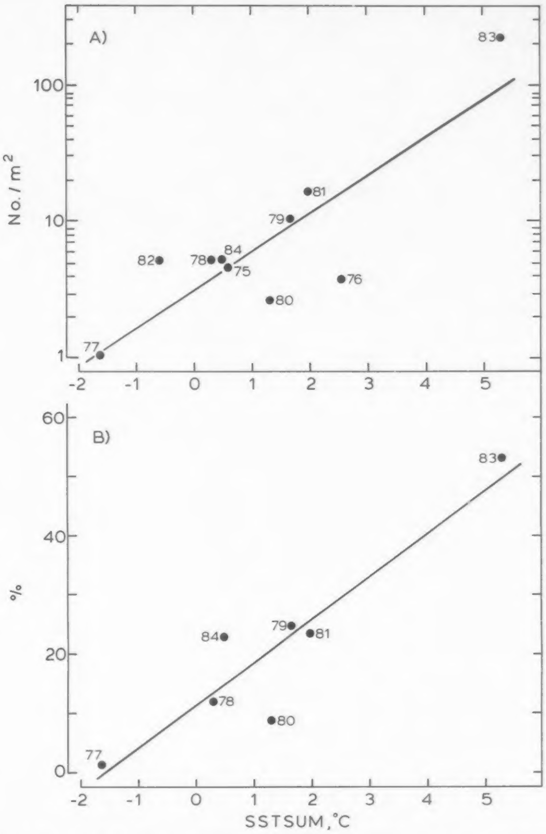

FIG. 8. (A) Relationship between spring abundance of *Pleurobrachia* and the sum of the monthly mean SST anomalies occurring from January to April (SSTSUM). (B) Relationship between the percentage of the *Pleurobrachia* population occurring in spring relative to the sum of its spring, summer, and fall abundance in the same year in the southwestern Nova Scotia region and SSTSUM.

The 8-yr record of ctenophore abundance data contained in Milne (1984) was largely derived from collections made either twice (March−April and October−November, 1975−82) or three times annually (March−April, July−August, and October−November, 1977−81) over the southwestern Scotia Shelf region where *Pleurobrachia* maintains a persistent center of abundance (Bigelow 1926). SST data for the Yarmouth subregion (43.0−45.0°N, 65.0−67.0°W; Trites and Drinkwater 1985a, 1985b), directly adjacent to Browns Bank, were taken to represent the hydrographic conditions influencing the study area. The spring abundance of *Pleurobrachia* (transformed to natural logarithms), including the data from my study, was regressed against the sum of the monthly mean SST anomalies occurring from January to April inclusive. This analysis yielded a significant positive relationship (Fig. 8) with the highest explained variance ($R^2 = 0.72$) relative to any other multiple combination of months from November to April or any month alone within this time period (range of $R^2 = 0.06 - 0.66$). The equation to predict the spring abundance of *Pleurobrachia* (y, number per square metre) is

$$(7)\quad \ln(y+1) = 1.16 + 0.648x, \qquad r = 0.85,\ n = 10,\ P < 0.01$$

where x is the sum of the monthly mean SST anomalies from January to April. An additional regression analysis was performed for those years when estimates of *Pleurobrachia* abundance were made three times annually (1977−81; this study: 1983−84). The equation to predict the proportion of the *Pleurobrachia* population (y, percent) occurring during the spring period is

$$(8)\quad \sin^{-1}(y)^{0.5} = 11.0 + 7.33x, \qquad r = 0.92,\ n = 7,\ P < 0.01$$

where x is the sum of the monthly mean SST anomalies from January to April (Fig. 8). Collectively, these analyses give added support to the hypothesis that temperature conditions in the sea surface layer during the overwintering period explain a significant proportion of the variance in the spring abundance of *Pleurobrachia*. Positive temperature anomalies were coupled with the advancement of the seasonal peak in ctenophore abundance from the summer to spring period. Temperature per se may not directly influence survival but covary with other environmental factors such as food supply, as was shown by Deason and Smayda (1982) who related the annual variation in the initiation and magnitude of pulses of *Mnemiopsis leidyi* (a lobate ctenophore) to zooplankton biomass in Narragansett Bay, Rhode Island. Exclusion of the 1983 data point from each analysis produced a reduction in the explained variance by 38% (eq. 7) and 30% (eq. 8); the spring abundance of ctenophores during 1983 exceeded all previous estimates in the 10-yr time series by 20-fold (Fig. 8). In light of this exceptional year, confirmation of Fraser's (1970) hypothesis will ultimately rest with the results from future monitoring of the region or evaluation of time series data on ctenophore abundance from other shelf regions, which at present appears to be generally lacking (e.g. no quantitative data exists on the species composition of gelatinous zooplankton on Georges Bank (Sherman et al. 1979; Davis 1984); the Scotian Shelf Ichthyoplankton Program (SSIP) during its extensive multiyear sampling effort did not record coelenterate abundance (O'Boyle et al. 1984)).

Possibly the relationship between SST anomalies and the spring abundance of *Pleurobrachia* is one of the underlying causes for the negative correlations between temperature (lagged to the birth year) and fish catch among the stocks of cod and haddock in the Gulf of Maine (Sutcliffe et al. 1977). The analysis of haddock catch is viewed with particular interest because the model used to predict catch included a lagged (3 yr = age of recruitment) temperature effect that was derived from a span of months from November to February. Since the annual timing of reproduction among many marine fish species occurs at a fixed date, with a standard deviation of approximately 1 wk (Cushing 1969), uncertainty exists as to whether or not the peak abundance of ctenophores will coincide with the peak hatching period for larvae. Exact phasing of the two components, such as that observed during the spring of 1983 on Browns Bank between haddock spawning and the *Pleurobrachia* bloom, might have been responsible for the low level of recruitment expected for the 1983 haddock year-class. However, Koslow et al. (1985) have dismissed this possibility because they calculated a daily rate of consumption by *Pleurobrachia* ranging from 0.4 to 0.9% of the prey standing stock. Their analysis of this potential effect was, however, inadequate for the following reasons: (1) consumption was not directly measured, rather it was based on the size-dependent clearance rates established for *Pleurobrachia* under experimental conditions at 13°C by Reeve and Walter (1976), (2) no size measurements were made on any of the ctenophores collected, and (3) clearance rates for marine zooplankton are strongly dependent on temperature (Reeve 1964; Huntley and Boyd 1984) and the ambient temperatures that ctenophores experienced in the region during their study ranged from 4 to 7°C. The average densities of *Pleurobrachia* on the bank in late April and May of 1983 were reported as 4.6 and $1.8/\mathrm{m}^3$, respectively (Koslow et al. 1985). Substitution of these values for the 1983 average value for N in Table 1 yielded daily prey removal rates of 26% in April and 10% in May, each of which exceeded their estimates by nearly two orders of magnitude.

The disproportionate effect of temperature on interactive populations has been previously documented for other ecosystems. For example, soft-shell clam (*Mya arenaria*) abundance is strongly limited by green crab (*Carcinus maenas*) and other predators which increase during periods of high SST; hence, soft-shell clam abundance is negatively correlated with SST (Dow 1972). Skud (1982) discussed a similar effect with respect to reciprocal oscillations in mackerel and herring abundance and environmental factors.

Finally, the controversy regarding whether or not *Pleurobrachia* is a significant component of the Scotian Shelf ecosystem (Browns Bank lying at the southwestern end) has arisen largely because of inadequate characterization of the pattern of ctenophore population fluctuations in the offshore region. Ctenophores were certainly a major component in the pelagic food web during the spring of 1983, consuming, on average, as much as 26% of the zooplankton standing stock daily in April and 10% in May, whereas during all of 1984 they were a minor component. Significant interannual variability in the timing of events in the ctenophore life cycle is a characteristic of *Pleurobrachia* inhabiting both coastal and shelf regions. The overwintering survival hypothesis, advanced to explain this pattern, may be the key life history insight derived from this study necessary to evaluate the dynamic ecological role of this species in the economy of offshore shelf waters.

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NOTES

Activity Differences Influencing Food Selection in the Marine Fish *Pomatoschistus microps*

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Magnhagen, C. 1986. Activity differences influencing food selection in the marine fish *Pomatoschistus microps*. Can. J. Fish. Aquat. Sci. 43: 223–227.

Diets of female and male *Pomatoschistus microps* during the reproductive period (May–July) differed. Males ate less but used a wider range of prey species than did females. While males guard the eggs and therefore are tied to a nest during the breeding season, females have a higher mobility which leads to a higher prey encounter rate and hence a higher food selectivity than in males. After reproduction the differences between the sexes in food intake and diet disappeared. In laboratory experiments the fish were less active in aquaria with a high prey density than in those with a low density. A decrease in food selectivity with an increasing prey density can thus be due to a decrease in the activity of the fish. At a high prey density, *P. microps* may benefit from having a low activity and taking unselectively the prey items in its vicinity. The advantages could be reduced detectability by predators and decreased energy expenditure due to locomotion.

On a observé des différences dans le régime alimentaire des mâles et des femelles de l'espèce *Pomatoschistus microps* au cours de la saison de reproduction (de mai à juillet). Les mâles ont mangé moins que les femelles mais ils ont utilisé un plus large éventail de proies. Alors que les mâles ont la garde des oeufs et sont par conséquent attachés à un nid, les femelles ont une plus grande mobilité, ce qui leur permet de rencontrer un plus grand nombre de proies et d'être ainsi plus sélectives dans le choix de leur nourriture. Une fois la saison de reproduction passée, on n'a plus observé de différences entre les sexes pour ce qui est de la ration et du régime alimentaires. Au cours d'expériences réalisées en laboratoire, les poissons se sont montrés moins actifs dans les aquariums où les proies étaient très nombreuses que dans ceux où les proies étaient en petit nombre. Par conséquent, il est possible qu'une diminution de la sélectivité dans le choix de la nourriture lorsque la densité des proies augmente soit attribuable à une baisse de l'activité des poissons. Lorsque la densité des proies est élevée, *P. microps* peut tirer parti du fait que son activité est faible et qu'il capture de façon non sélective les proies qui se présentent dans son voisinage. Les avantages pourraient être une moins grande possibilité de détection par les prédateurs et une diminution de la dépense d'énergie due à la locomotion.

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To optimize its feeding, an animal can use one of several foraging strategies, appropriate for different species, environments, etc. In addition to the first foraging theories (Schoener 1971; Pyke et al. 1977) a number of different strategies to achieve optimality have recently been discussed, such as benefit maximization, time minimization, cost minimization, and activity minimization (Fagerström et al. 1983; Sih 1984). As prey density increases, food selectivity should increase according to simple foraging theories. The response of a predator to prey density, however, must depend on its "goal," i.e. what parameters the predator tries to maximize or minimize (Sih 1984). Change in predator activity with changing prey abundance has been predicted by several authors (Ware 1975; Gerritsen and Strickler 1977; Norberg 1977), but the predictions differ in the direction of the change. Norberg (1977) assumed an increase in the activity of the predator whereas Gerritsen and Strickler (1977) predicted a decrease with increasing prey density. Ware (1975) made different predictions for benefit maximizers and benefit/cost maximizers. In the former case the optimal hunting speed would increase up to a prey density threshold and then decrease, but in the latter case the speed should always decrease with increasing prey density. With increasing activity, prey encounter rates increase, but so do the energetic costs of foraging. Thus the energetic expenditures were 1.3–1.5 times greater for a widely foraging lizard compared with a sit-and-wait lizard (Huey and Pianka 1981). These lizards, however, were of different species, but in a few species, individuals were found to change their foraging mode in accordance with food density.

The common goby *Pomatoschistus microps* (Krøyer) is a marine benthic fish, occurring in great numbers on shallow soft-bottom areas along the coast of Sweden. It feeds mostly on infauna, and in my field study area especially on the amphipod *Corophium volutator* (Pallas) (Magnhagen and Wiederholm

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TABLE 1. Stomach contents of females and males of *P. microps* taken from Kilviken Bay. Mean numbers and frequency of occurrence (%*F*) of the different prey types and stomach fullness of the fishes are given. Twenty-five fishes of each sex were analysed in May and July and 20 in August.

	Females		Males	
Stomach contents	$\bar{X}$ (SD)	%*F*	$\bar{X}$ (SD)	%*F*
28 May				
Corophium	4.9 (4.7)	84	0.6 (0.8)	44
Chironomids	0.7 (0.7)	56	0.2 (0.4)	20
Nereis	0.2 (0.4)	16	0.1 (0.3)	8
Harpacticoids		8		48
Stomach fullness %, median value (range)	80 (0–100)		10 (0–50)	
13 July				
Corophium	8.3 (6.0)	92	1.7 (1.2)	83
Chironomids	0.4 (0.5)	36	0.2 (0.4)	17
Nereis	0.5 (0.5)	52	0.2 (0.4)	17
Harpacticoids		0		33
Ostracods		0		33
Stomach fullness %, median value (range)	90 (0–100)		50 (0–100)	
17 August				
Corophium	2.2 (2.3)	75	1.9 (1.7)	75
Chironomids	0.1 (0.4)	15	0.1 (0.3)	10
Nereis	0.4 (0.7)	35	0.5 (0.7)	45
Harpacticoids		15		10
Ostracods		60		35
Stomach fullness %, median value (range)	50 (10–90)		50 (0–100)	

1982). *Pomatoschistus microps* is a suitable species for studying effects of activity on food choice because of different activity patterns in females and males during the breeding season associated with their different reproductive roles. In *P. microps*, as in other gobiid fishes, parental care occurs. The male builds a nest consisting of a burrow under a bivalve shell. The adhesive eggs are deposited at the ceiling and the female departs after spawning. The eggs are guarded and fanned by the males until hatching (Nyman 1953). Males leave their nests only for short feeding bouts and to chase away intruders (C. Magnhagen, pers. obs.). During the reproductive period (May–July), therefore, the females can be more mobile (i.e. more wide ranging) than can the males.

In a feeding experiment when *P. microps* was offered different densities of three size-classes of *Corophium*, Magnhagen (1985) found that at the lowest prey density the fish were highly selective in favour of large prey. As the density of smaller size-classes increased, however, the food intake became random. I suggested that this resulted from a decrease in activity as prey density increased. The unselective food intake produced a lower energy intake compared with the selective feeding in low-density aquaria. On the other hand, a decrease in activity should have lowered the energy cost for foraging, and it might also be an important strategy to avoid predators. The fish thus seem to behave as cost or activity minimizers according to Sih's (1984) definitions. In this note, I have examined the connection between mobility and food selectivity in *P. microps* by looking at two aspects: (1) Does a decrease in food selectivity due to higher prey density depend on a decrease in activity by the fish? (2) Does the decrease in mobility (i.e. search range) in males during reproduction lead to a change in diet?

Materials and Methods

Field samples were taken in Kilviken Bay in Gullmar Fjord on the west coast of Sweden (58°15′N, 11°28′E). Fish were caught on 28 May, 13 July, and 17 August 1984 at a depth of about 0.5 m using a handtrawl. The fish were preserved in 70% alcohol, the sexes separated, total length measured, and stomach analyses were made of 25 fishes of each sex in May and July and 20 in August. Food items were classified and counted, and the degree of stomach fullness was estimated using a scale 0–100% with 10% intervals. In May and July, all fishes were sexually mature. In August, most of them were juveniles, and only those whose sex could be determined on external features were used.

Activity experiments were carried out at Kristinebergs Marine Biological Station, Fiskebäckskil, Sweden, in July 1984. The activity of *P. microps* at different prey densities was measured as the number of passages across an infrared beam in two double-walled octogonal aquaria with a diameter of 60 cm and a bottom area of 16 dm^2. Water flow was continuous and muddy sand was used as bottom substrate. Water temperature was 14–17°C. Only natural daylight was used in the laboratory, and therefore light conditions differed between days. *Corophium* with a length of 4–6 mm were employed as prey. In one of the aquaria, I introduced 150 (approximately 1000/m^2) and in the other 600 (approximately 4000/m^2) *Corophium*. Comparatively, in the field there were about 1000 *Corophium*/m^2 of that size-class in May and about 3000/m^2 in June 1984 (C. Magnhagen, unpubl. data). The *Corophium* were given enough time to bury themselves before

TABLE 2. Results of MANOVA testing the influence of sex and time period on number of prey of different species eaten by *P. microps* (ns = not significant).

		Corophium		Chironomids		*Nereis*	
	df	*F*	*P*	*F*	*P*	*F*	*P*
Sex	1	41.0	<0.001	9.4	<0.01	0.2	ns
Period	2	7.4	<0.001	4.7	<0.01	6.2	<0.01
Sex × period	2	7.7	<0.001	2.8	ns	1.2	ns

TABLE 3. Results of Duncan's multiple range test on differences between sex and period in number of prey eaten by *P. microps*. Test on the MANOVA in Table 2. Means followed by the same letter are not significantly different.

Variables	Mean	Sex	Mean	Month
Corophium	5.13 a	♀	2.85 b	May
	1.40 b	♂	4.75 a	June
			2.07 b	August
Chironomids	0.40 a	♀	0.44 a	May
	0.15 b	♂	0.24 ab	June
			0.12 b	August
Nereis	0.34 a	♀	0.12 a	May
	0.26 a	♂	0.32 ab	June
			0.50 b	August

the experiments were begun. The fish were deprived of food for 24 h. The experiments were each run for 1 d. Four fish were put in each aquarium at 08:00. After the fish adjusted to the environment for 2 h, the activity (i.e. number of passages through the infrared beam) was registered every other hour until 24:00. Every other day, new prey were added, 20 to the low-density aquarium and 40 to the high-density aquarium. The experiments were repeated 16 times. Only females were used in these experiments so that any mating activity or differences between the sexes would not affect the results.

Results

Females had a higher degree of stomach fullness than males in May and July (Mann-Whitney, two-tailed; $P < 0.001$) (Table 1). No difference was found in August. In May, *Corophium* and chironomid larvae occurred more frequently in females than in males (χ^2; $P < 0.01$ and $P < 0.02$, respectively) and harpacticoid copepods were more frequent in males (χ^2; $P < 0.01$). In July, frequency of occurrence ($\%F$) of *Nereis* was higher in females (χ^2; $P < 0.02$), while harpacticoids and ostracods were eaten by males only. In August no differences between the sexes in $\%F$ of any prey items were found. The simultaneous influence of sex and time period on the number of *Corophium*, chironomids, and *Nereis* eaten by the fish was tested (Tables 2 and 3). For *Corophium* and chironomid larvae, both the sex of the fish and the period had a significant influence on the number of individuals eaten, and for *Corophium* there was an interaction between the two factors. In *Nereis*, only the period influenced the number of prey items eaten. The females consumed a significantly higher number of *Corophium* and chironomid larvae compared with the males (Table 3). Furthermore, the mean number of ingested chironomids decreased and the number of *Nereis* increased in the diet from spring to late summer.

The length distributions of the sexes were equal in May ($\bar{X}$ (SD) mm): ♀ = 34.1(3.0), ♂ = 34.8(3.8) (Fig. 1). In July, females were significantly larger (♀ = 41.6(3.3), ♂ = 36.8(2.7)) (Mann-Whitney, two-tailed; $P < 0.001$). Again, in August there was no difference (♀ = 34.5(5.0), ♂ = 33.7(3.8)), but then most of the fish belonged to the 0+ age-group and few of the 1+ group still remained.

Activity, measured as the mean number of passages across the infrared beam, was higher in the aquarium with low prey density than in the high-density aquarium (Fig. 2). The high standard deviations probably are the result of both individual differences and variable light conditions on the subsequent days. However, when comparing the data pairs (e.g. the data from high- and low-density aquaria taken the same time and day), the difference was highly significant (Wilcoxon; $P < 0.001$).

Discussion

The aim of this study was to test the hypothesis that individuals of the same species select prey differently depending on their activity. In *P. microps*, different reproductive behaviour in males and females, as well as changing prey densities, should lead to a variability in food search activity and hence to different diets within the species.

Feeding habits differed between females and males of *P. microps* during the breeding season. The diet of the females was largely restricted to *Corophium*, chironomid larvae, and *Nereis*. The males also ate harpacticoid copepods and ostracods, which are considerably smaller than the other prey items, but much less of the larger prey, especially *Corophium*, than did the females. This difference probably resulted from the males' restricted range for food search because they were guarding the nest. Their prey encounter rate therefore was considerably lower compared with the females which probably were more mobile. Males were constrained to take whatever prey items were available in the vicinity of the nest and could not "afford" to be selective. Similarly, male *Padogobius martensi* (Gobiidae) spend very little time outside the nest looking for food, especially during the last days before hatching (Torricelli et al. 1985). Five nearshore fishes, including *P. microps*, had wider food niches during the breeding season than otherwise (Thorman and Wiederholm 1983). The increase in food niches was explained as resulting from limiting search time and area due to territorial behaviour. These results support the ones in my study even though the diets of the sexes were not separated. Male hogfishes (*Bodianus* spp.) allocated a much smaller proportion of their time to foraging than did conspecific females (Hoffman 1983). The reproductive success in the males depended more on social and mating activities than net energy gains, while the opposite was true for females. Similarly, in the reef fish *Eupomacentrus leucostictus* the two sexes had different feeding strategies (Ebersole 1980). Females behaved as food maximizers and expanded their territories

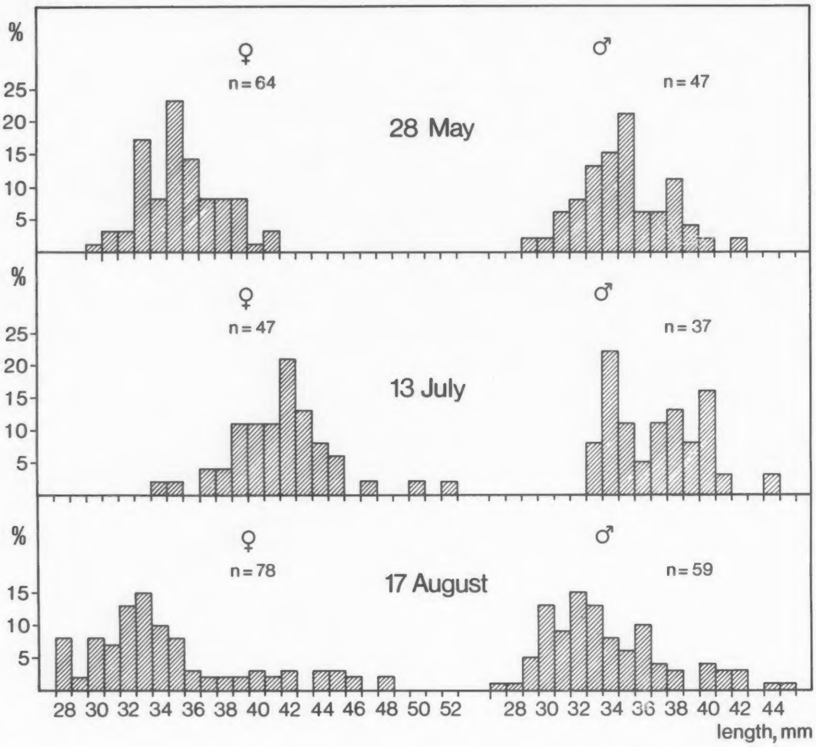

FIG. 1. Size distribution of females and males of *P. microps* taken from Kilviken Bay. Juveniles on which the sex was not externally distinguishable were not included.

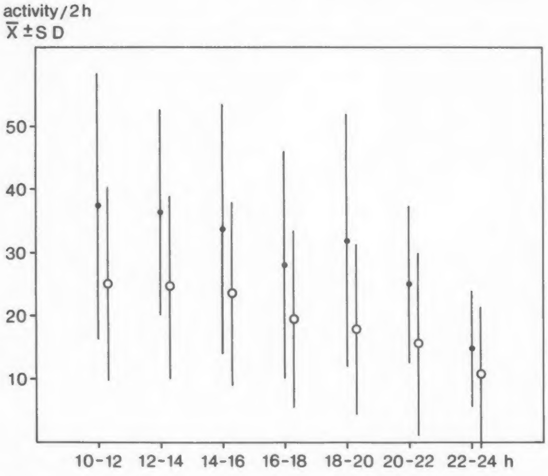

FIG. 2. Activity of *P. microps* measured as number of passages per 2 h by four fishes through an infrared beam. Means and standard deviations of 16 runs are given. ○ = high prey density (600 *Corophium*/aquarium); ● = low prey density (150 *Corophium*/aquarium)

when food density increased. The extra food thus obtained was used to produce more egg biomass, or to increase the growth rate which ultimately leads to the production of more eggs. The males, on the other hand, had no need for food beyond what was needed for body maintenance, and either maintained or contracted their territory size as prey density increased. The fish species in both these studies had patterns similar to *P. microps*, namely that the two sexes differed in feeding strategy.

In July, male *P. microps* were on average smaller than females, which probably stemmed from a reduced growth rate during the breeding season owing to the lower food intake. When parental investment is studied, it is usually the energy the parent puts into the progeny that is discussed (Baylis 1981), but in *P. microps* the situation is different. The males lowered their energy intake, and as a result of this the survival of the eggs probably increased. The question of whether or not the lower energy intake and growth rate in males represents a cost of reproduction of course depends on its effect on the males' fitness, specifically on their survival rate and on their chance to breed a second season. *Pomatoschistus microps* has a life span of about 1.5 yr, and only one breeding season (Miller 1975). It is thus most important that the survival of the eggs is high. Males should spend as much time as possible guarding the eggs, and feed just to survive the breeding season, because they would have little to gain by growth. For females, on the other hand, growth is more important because a large female can produce more eggs than a small female, and individual fish spawn several times during the breeding season (Miller 1984).

In August there was no difference in the diet of females and males. Both sexes were then feeding on the wide range of prey exploited in May and July by the males only. This can depend on changes in the food abundance or on the increase in fish density due to the recruitment of juveniles (compare e.g. Miller 1975) leading to intraspecific competitive interactions and hence influencing the foraging behaviour. This, however, has not been studied in this case. Another explanation could be that predation pressure increased in August, to which the fish may have responded by decreasing their activity, and hence their prey encounter rate, to lower their own detectability for fish predators. Pihl (1982) found an increasing predation on *Pomatoschistus* spp. by cod (*Gadus morhua*) in the autumn in a bay in Gullmar Fjord, which might support this hypothesis.

Decreased selectivity in *P. microps* with increasing prey density was found in laboratory experiments (Magnhagen 1985), which contradicts predictions made from current optimal foraging theory. However, predictions of feeding behaviour should differ in accordance with the goal of the forager (Sih 1984). In contrast with an energy maximizer, animals using other feeding strategies may be aiming at gaining a threshold benefit while minimizing some other factor such as time, activity, or cost in terms of energy expenditure and risk of mortality. For a cost or activity minimizer the activity should decrease with increasing food density, as has been shown for *P. microps* in this study. Advantages of a low activity include reduced predation risk (*P. microps* is cryptic and difficult to detect when immobile) and reduced energy expenditure for locomotion. The critical energy intake/cost threshold might be reached at a high prey density even if the fish unselectively catches any prey item in its vicinity.

In conclusion, I have shown that prey density can influence the activity of *P. microps*; with increasing prey density its activity decreases. Furthermore, the amount of activity of the individual fish influences its prey selection; specifically, low activity leads to unselective prey capture. Thus, both nest guarding in males and a high prey density lead to decreasing food search activity and hence to unselective foraging.

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Histological Changes in Cultured Lake Trout, *Salvelinus namaycush*, Subjected to Cumulative Loading in a Water Reuse System

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Lake trout (*Salvelinus namaycush*), 16 cm long, were reared 8 wk in five serial reuse units, resulting in cumulative loadings of 1.5–7.5 kg fish$\cdot$L$^{-1}\cdot$min^{-1}. Although mean un-ionized ammonia concentrations in the highest loading levels were less than 10% of those often considered as safe for culture of rainbow trout (*Salmo gairdneri*), lake trout reared at the higher loading levels showed dilation of glomerular capillaries, a condition that persisted after cumulative loading conditions were removed, and gill epithelial hyperplasia and hypertrophy. We observed lamellar telangiectasis caused by sampling technique. We conclude that parameters other than ammonia concentrations are significant factors in branchial irritation.

Des touladis (*Salvelinus namaycush*) mesurant 16 cm ont été élevés pandant 8 sem dans cinq bacs en série où l'eau est réutilisée, ce qui a entraîné des charges cumulatives allant de 1,5 à 7,5 kg de poisson$\cdot$L$^{-1}\cdot$min^{-1}. Bien que les concentrations moyennes d'ammoniac non ionisé dans les niveaux de charge les plus élevés aient été inférieures à 10 % de celles que l'on considère souvent comme sécuritaires pour l'élevage de la truite arc-en-ciel (*Salmo gairdneri*), il y a eu dilatation des capillaires des glomérules du rein chez les touladis élevés à des niveaux de charge élevés, condition qui s'est maintenue même après qu'il n'y ait plus eu de charges cumulatives, ainsi qu'une hyperplasie et une hypertrophie du tissu épithélial des branchies. Nous avons observé des cas de télangiectasie lamellaire dus à la technique d'échantillonnage. Nous concluons qu'il y a d'autres paramètres que les concentrations d'ammoniac qui jouent un rôle important dans l'irritation des branchies.

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In flow-through fish culture systems, such as those commonly used in salmonid husbandry, the first limitation to production encountered is available dissolved oxygen in the source water. When the oxygen constraint is overcome, the accumulation of metabolites becomes the limiting factor for production (Colt and Armstrong 1981). Effects of metabolites on salmonids are not fully understood, and effects on lake trout (*Salvelinus namaycush*) have not been described. Meade (1985) conducted studies on the effects of loading (weight of fish per unit of flow) on lake trout in a serial reuse system with supplemental aeration to eliminate oxygen as a limiting factor. Because histopathology has been reported in rainbow trout (*Salmo gairdneri*) reared in serial reuse systems (Larmoyeaux and Piper 1973) and in salmonids exposed to experimental levels of ammonia, histological examination of selected tissues was included in the study.

Our objective was to determine histopathology associated with total metabolite accumulations on lake trout reared in an aerated, serial reuse water system and its potential as one measure of fish quality.

Materials and Methods

Lake trout were from the Clearwater Lake (Manitoba) strain. The water supply had a total hardness of 40 mg$\cdot$L^{-1}, a pH of 6.5–8.0, and a mean temperature of 8.5°C. Three replicates, in series, of five epoxy-coated fiberglass tanks with a volume of 390 L (180 × 57 × 38 cm) were used as rearing units. Water, at a rate of 19 L$\cdot$min^{-1}, from each rearing unit entered a 75-L fiberglass tub, was reaerated to 90% of oxygen saturation, and then flowed into the next rearing unit. A total of 28.5 kg of lake trout (16 cm mean total length) were placed in each of the rearing units, at a loading rate of 1.5 kg$\cdot$L$^{-1}\cdot$min^{-1}. After 9 d of acclimatization, fresh water to all units, except the first, was gradually turned off and replaced by used, reaerated water from upstream units, resulting in accumulative loads of 1.5, 3.0, 4.5, 6.0, and 7.5 kg$\cdot$L$^{-1}\cdot$min^{-1}. The water changeover required about 6 h. The test period of 8 wk was followed by 8 wk of recovery during which only fresh water was supplied to each unit. Fish were fed U.S. Fish and Wildlife Service formula GR 6-30 at 300 g$\cdot$d$^{-1}\cdot$unit^{-1}. Proximate analysis of the feed was 42.6% protein, 14.8% fat, and 9.5% moisture (Ivan McElwain, Northeast Fisheries Center, Lamar, PA, pers. comm.).

We readjusted the weight of fish in each unit by removing enough fish every 14 d to reduce total weight to 28.5 kg. Fish for histological examination were preserved on d 0, 2, 6, 14, 28, 42, and 56 of rearing during the cumulative loading period

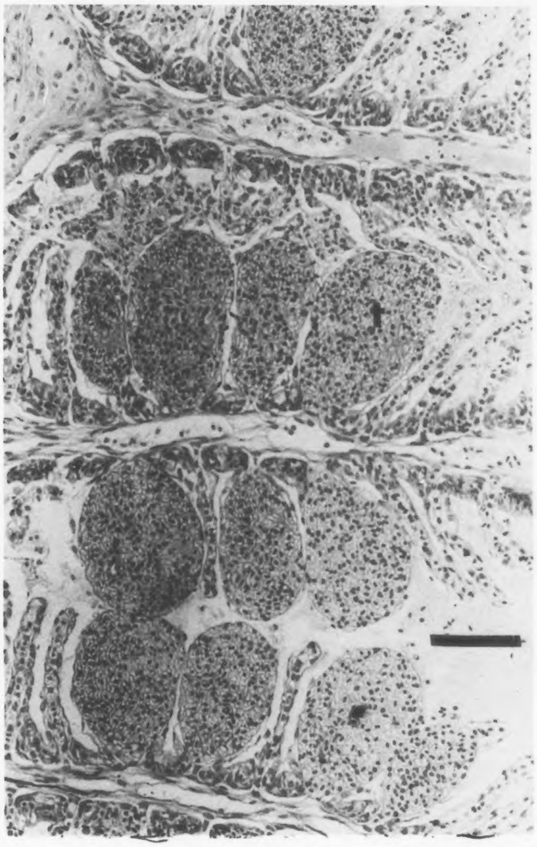

FIG. 1. Section of lake trout gill from pretest sample showing severe telangiectasis (t) at the base of filaments. Bar = 50 μm.

and on d 14, 28, and 49 during the period of recovery conditions. Fish to be sampled were killed by a blow to the head, weighed and length measured, and blood samples taken for chemical analysis and then six were fixed in Bouin's solution for 12−36 h and stored in 65% alcohol. Fish were not histologically sampled from all units at each time period. For comparison testing, samples of four strains of lake trout were obtained from production lots at the Allegheny National Fish Hatchery (Pennsylvania).

Gills, kidney, and liver with associated visceral tissues were embedded in paraffin, sectioned at 4 μm, and stained with hematoxylin and eosin. Selected sections were stained with Novelli for mitochondria (Novelli 1955) and MacCallum−Goodpasture for bacteria. Oxygen, ammonia, pH, alkalinity, conductivity, and temperature were monitored daily during wk 1 of the test and weekly thereafter. On two occasions, ammonia was measured hourly during a 24-h period (Meade 1985).

Results

Un-ionized ammonia (NH_3) averaged 0.001 $\mathrm{mg \cdot L^{-1}}$ or less in all units within each 2-wk period. The highest recorded NH_3 level was 0.003 $\mathrm{mg \cdot L^{-1}}$.

Gill lesions were common in fish examined, including those from hatchery stocks. Separation of the epithelium from underlying basement membrane with and without edema was present to some degree in nearly 100% of the gills examined. Telangiectasis (Fig. 1) was seen in about 30% of all gills sectioned. Epithelial hypertrophy (Fig. 2) was characteristic of gill tissue from fish at loading levels of 6.0 and 7.5 $\mathrm{kg \cdot L^{-1} \cdot min^{-1}}$ from d 6 through 8 wk. Cellular debris (residual bodies) and macrophages contraining debris were also common in these gills, particularly on d 6. The gills of fish sampled at 8 wk from loading level 7.5 $\mathrm{kg \cdot L^{-1} \cdot min^{-1}}$ showed scattered areas of lamellar fusions (Fig. 3). These sections were negative for bacteria.

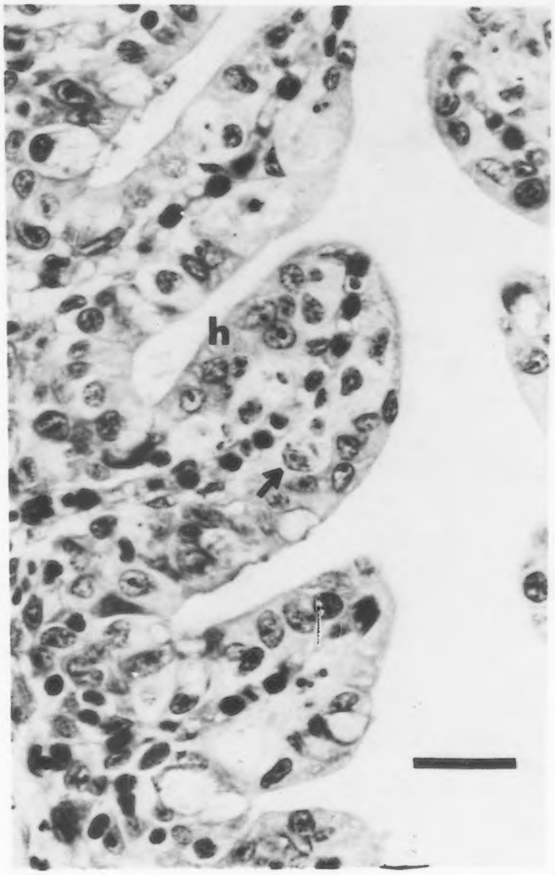

FIG. 2. Hypertrophy of gill epithelial cells (h) and debris-laden macrophages (arrow) of lake trout after 8 wk at 7.5 $\mathrm{kg \cdot L^{-1} \cdot min^{-1}}$ cumulative loading. Bar = 25 μm.

Capillary dilation in the glomerular tufts increased with loading level (Fig. 4). At loading level 7.5 $\mathrm{kg \cdot L^{-1} \cdot min^{-1}}$, renal sinusoids also tended to be dilated. Proteinaceous precipitates were noted in tubular lumina at all loading levels. Hepatic vacuolization was as variable within groups as between groups, showing no obvious relation to loading levels.

Gill samples taken during recovery indicated rapid regression of pathological changes; all sections appeared normal within 2 wk. In kidneys of some fish in the last sample (7 wk postload), from levels 6.0 and 7.5 $\mathrm{kg \cdot L^{-1} \cdot min^{-1}}$, capillaries in the glomeruli were still dilated, indicating that recovery was much slower in renal tissue than in gills.

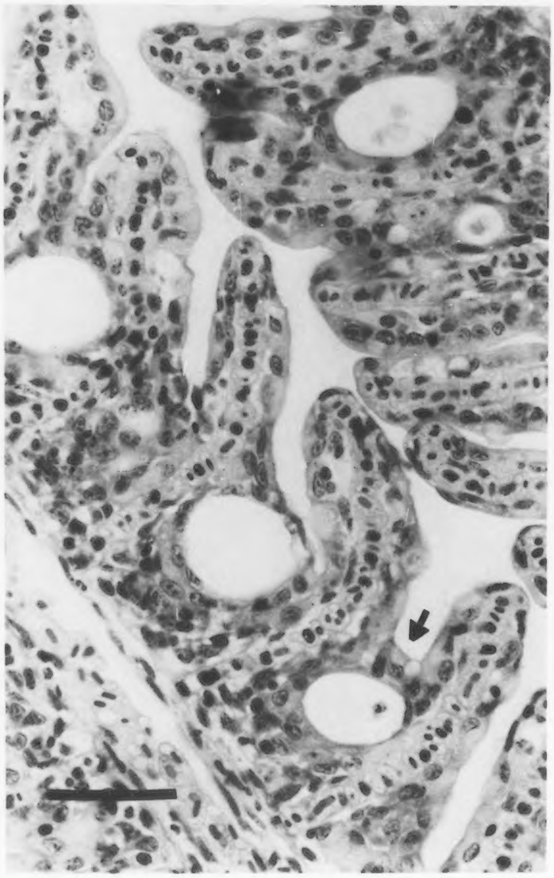

FIG. 3. Section of lake trout gill showing lamellar fusion (arrow) after 8 wk at 7.5 kg·L^{-1}·min^{-1} cumulative loading. Bar = 50 μm.

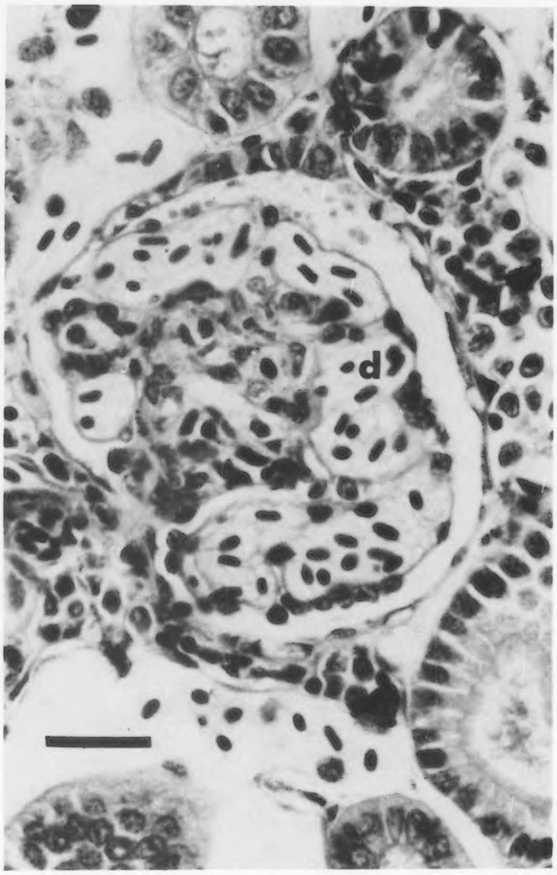

FIG. 4. Section of lake trout kidney showing dilated glomerular capillaries (d) after 8 wk at 7.5 kg·L^{-1}·min^{-1} cumulative loading. Bar = 25 μm.

Discussion

Telangiectasis has been reported to result from exposure to ammonia (Bullock 1972; Smith and Piper 1975; Smart 1976; Thurston et al. 1984). In the present study, however, telangiectasis was very likely an artifact resulting from killing the fish by a blow to the head. This was confirmed by Herman and Meade (1985), who demonstrated that these lesions could easily be produced in lake trout by a blow to the head, while rainbow trout and Atlantic salmon (*Salmo salar*) appeared to be less susceptible.

The separation of the epithelium from the pillar cells tended to be more severe toward the filament bases and may have been an artifact caused by oxygen deficiency before penetration of the fixative, possibly a result of fixing fish whole. Edema was nearly always associated with the telangiectasis and also may have resulted from the trauma of concussion.

Because of the strength of eosin staining, hypertrophy of the gill respiratory epithelium was initially believed to be due to proliferation of mitochondria, but results of Novelli staining did not support this hypothesis. The condition was similar to that reported by Daoust et al. (1984), where exposure to heavy metals was associated with hypertrophy of gill epithelial cells accompanied by increased numbers of lysosomes. Kudo and Kimaru (1983a, 1983b) also noted lysosomes and other indications of cellular breakdown in studies of bacterial gill disease. Thurston et al. (1984) found that epithelial hypertrophy increased with increases in ammonia. In our study, ammonia concentrations were low in all units and the hypertrophy was seemingly initiated by some other factor.

Lake trout did not show the inclusions in the proximal tubules reported by Daoust and Ferguson (1984) and Thurston et al. (1984). Such inclusions are usually protein resorbed after stress-induced leakage across the glomeruli. The capillary dilation in the glomeruli did indicate some effect on kidney function.

The lamellar fusion noted in samples taken in wk 8 from the 7.5 kg·L^{-1}·min^{-1} loading level appeared to be formed by bridging of the epithelial cells from one lamella to another. Fusion of lamellae by contact is common in bacterial gill disease and has been reported to result from exposure to heavy metals (Daoust et al. 1984). The absence of demonstrable bacteria in the sections examined after 8 wk does not preclude the possibility that the fish were suffering from low-grade bacterial gill disease.

Although many pathological changes (telangiectasis and edema) that we saw were probably attributed to the sampling technique (concussion), there was significant evidence of tissue damage associated with loading levels despite oxygen and NH_3 levels being within generally accepted safe limits for salmonid culture. These results indicate that ammonia is not the only possible cause of branchial irritation of fish under intensive culture conditions and other factors should be examined.

Acknowledgments

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Aluminum Speciation in Some Synthetic Systems: Comparison of the Fast-Oxine, pH 5.0 Extraction and Dialysis Methods

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Lalande, H., and W. H. Hendershot. 1986. Aluminum speciation in some synthetic systems: comparison of the fast-oxine, pH 5.0 extraction and dialysis methods. Can. J. Fish. Aquat. Sci. 43: 231–234.

A procedure for the fractionation of aqueous aluminum was evaluated on synthetic systems using 8-hydroxyquinoline (oxine) at pH 5.0 or 8.3 and reaction times of 15 s or 60 min. For comparison of the speciation of the most reactive forms of Al, dialysis tubing with a molecular weight cutoff of 1000 was used. In the hydroxide and fluoride systems the fast-oxine, pH 5.0 method clearly distinguishes between different forms of Al. In systems containing citrate and oxalate, low molecular weight organic complexing agents, the fast-oxine method produced a clearer distinction between inorganic and organically complexed Al than did the dialysis method. In contrast, the Al species in systems containing fulvic acid and leaf litter leachate were much more clearly differentiated by the dialysis method. The fast-oxine, pH 5.0 reaction appears to extract a fraction of the organically complexed Al; this supports the hypothesis that natural organic complexes have a wide range of bond strengths to metal ions.

Une méthode de spéciation est appliquée sur plusieurs systèmes purs en se basant sur la cinétique de réaction de l'aluminium avec le 8-hydroquinoline (oxine), à deux pH différents, 5.0 et 8.3, et à des temps de réaction de 15 s et 60 min. Afin de comparer la spéciation des formes les plus réactives, une membrane de dialyse est utilisée, permettant ainsi la séparation des molécules de poids inférieur à 1000. Dans les systèmes d'hydroxides et de fluorures, la méthode de l'oxine à pH 5.0, 15 s distingue clairement les différentes formes d'Al. Sur les systèmes composés de citrate et d'oxalate d'Al, complexes organiques de faible poids moléculaire, la spéciation à pH 5.0 permet une meilleure distinction entre les complexes organiques et inorganiques d'Al que la méthode de dialyse. Par ailleurs, les formes d'Al dans les systèmes à base d'acides fulviques et de lessivat de litière sont beaucoup mieux différenciées par la procédure de dialyse. La méthode de l'oxine au pH de réaction de 5.0 semble extraire une partie de l'Al complexé aux molécules organiques; ce qui tend à montrer la grande diversité de liens qui existent entre les complexes organiques et les ions métalliques.

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The decrease in fish populations observed in eastern North America has been attributed to a decrease in pH combined with an increase in dissolved aluminum (Schofield 1976; van Coillie et al. 1983). However, the amount of total dissolved Al does not provide a good indication of toxicity. The aquo-ion of Al (Al^{3+}) and the highly reactive, monomeric hydroxo-complexes are considered to be responsible for the toxic conditions in natural soft acidified waters, while more complex molecules, polymers, and organically complexed Al, which are less reactive, have no significant effect (Driscoll et al. 1980; Baker and Schofield 1982). According to these authors the fluoro-complexes are less toxic than Al^{3+} and the hydroxo-complexes although they may be toxic to some species (Clark and LaZerte 1985). In order to assess the quality of an aquatic environment it is clearly essential to measure not only the total dissolved Al content and pH but also the quantity of the different forms of Al.

A number of authors have presented procedures that operationally separate Al into different forms (Driscoll et al. 1980; Campbell et al. 1983; Driscoll 1984; LaZerte 1984; Seip et al. 1984). These methods attempt to accurately measure the concentration of monomeric inorganic Al due to its threat to the aquatic environment. Methods using 8-hydroxyquinoline (oxine) to determine labile or reactive Al have been proposed for use in natural waters (Turner 1969, 1971; Barnes 1975; Bloom et al. 1978; James et al. 1983). One problem with the oxine reagent is that it does not clearly distinguish between monomeric inorganic and organic forms of Al. LaZerte (1984) proposed the use of a dialysis membrane with a molecular weight cutoff of 1000 to make this distinction. The method proposed here employs the oxine reaction at two pH values, 5.0 and 8.3, to separate the aquo- and hydroxo-complexed forms of Al from the fluoro- and organo-complexed forms. This note outlines a modified method for Al speciation that is simple and requires a minimum of equipment. In environmental studies this method can be employed to separate Al into three operationally defined reactivity classes. The method requires three measurements of Al concentration: Al_1, the fast-oxine (15 s), pH 5.0 reaction; Al_2, the fast-oxine (15 s), pH 8.3 reaction; and Al_3, the slow-oxine (60 min), pH 8.3 reaction.

Methods and Materials

Reagents

0.8% oxine solution: 8 g of hydroxyquinoline dissolved in 25 mL of glacial acetic acid and diluted to 1 L; stored in the dark.

1 *M* sodium acetate buffer solution: 136.1 g of $NaOAc \cdot 3H_2O$ dissolved and diluted to 1 L. This buffer gives a pH during the oxine reaction of 5.0.

10 *M* ammonium acetate stock solution: 770.8 g of NH_4OAc dissolved and diluted to 1 L.

5 *M* ammonium acetate buffer solution: 50 mL of 10 *M* NH_4OAc stock solution pipetted into a 100-mL volumetric flask, 5.8 mL of concentrated ammonium hydroxide added, and diluted to volume. This buffer should give a reaction pH of 8.3; this must be checked every time the solution is prepared and the amount of NH_4OH adjusted if necessary. Make fresh daily.

n-butyl acetate: reagent grade.

Procedure — Twenty-five millilitres of sample solution or standard was pipetted into a 20 × 150 mm borosilicate screw-top culture tube with a teflon-lined cap. One millilitre of oxine solution and 1 mL of the appropriate buffer solution were added simultaneously using piston pipettes. The tube was capped and shaken vigorously for 10 s. The reaction was stopped and the Al−quinolate extracted at the desired time (15 s or 60 min) by adding 5 mL of *n*-butyl acetate, recapping the tube, and shaking vigorously. The tube was then allowed to stand for at least 15 min while the aqueous and nonaqueous (*n*-butyl acetate) phases separated. The absorbance of the nonaqueous phase was measured at 395 and 600 nm using a Perkin-Elmer Lambda 1 spectrophotometer. A correction factor to eliminate the positive interference at 395 nm due to the Fe−quinolate complex was calculated from the absorbance of this complex at 600 nm. The detection limit (3 × standard deviation of the blank divided by the slope) was calculated as 0.007 mg Al/L and the analytical precision was calculated as being the larger of 5% or 0.005 mg Al/L (95% confidence limit, 10 replicates at 0.020 and 0.400 mg Al/L).

Dialysis — The method outlined by LaZerte (1984) was followed. The dialysis tubing, Spectrapor 6, 1000 molecular weight cutoff (mwco), 11.5 mm in diameter, was used with a volume ratio of between 2 and 4% v/v. The tube was filled with distilled, deionized water and allowed to equilibrate with the sample solution for 24 h at 25°C. The solution inside the tube (dialysate) was analysed using the fast-oxine, pH 8.3 extraction.

Preparation of the synthetic systems — The synthetic systems were all prepared from $AlCl_3$ and, except for the leaf leachate, had 0.27 mg Al/L (0.01 m*M*), a concentration that can be expected in natural acidic waters in parts of southern Quebec (Hendershot et al. 1984). For each of the synthetic systems, enough of the complexing agent (anion) was added to give an equivalents ratio of Al:counterion of 1:4. The excess ligand was added to promote the formation of the Al complex. The solutions containing the fluoride or organic complexing agents were first adjusted to pH 3.0 with HCl and the Al added. This procedure was used to prevent the formation of polynuclear hydroxy-Al species prior to complex formation with the ligand. The pH of the solution was then slowly raised to 5.0 by adding a dilute $NaHCO_3$ solution while mixing rapidly with a magnetic stirrer. Finally the solution was made up to volume. The analyses were completed within 48 h after preparation of the solutions.

The fulvic acid was from the Armdale soil and is discussed more fully in Mak and Langford (1983). The leaf litter leachate was prepared by extracting 60 g of L horizon, taken from an Orthic Humo-Ferric Podzol at St-Hippolyte, Quebec, in 800 mL of distilled, deionized water. After centrifugation (500 × *g* for 15 min) the solution was filtered through a 0.2-μm polycarbonate filter. The filtered solution was further diluted with distilled, deionized water (one part leaf leachate to four parts H_2O) to prepare the test solutions. To this solution, 0.20 mg Al/L was added. The speciation of Al was measured on both the original solution and the solution containing the added Al; only the results of the difference between the two solutions are presented.

Results and Discussion

The results of the dialysis separation are calculated by using the amount of fast-oxine, pH 8.3 Al found inside the tube as a measure of the monomeric Al other than that in organic complexes. The results are therefore presented as fractions A and B, which are the amounts of monomeric Al in the inorganically complexed and organically complexed forms, respectively

TABLE 1. Results of the speciation of Al in the synthetic systems by the two methods (mg/L).

Sample	Dialysis		Oxine reaction			
	Fraction A	Fraction B	Class I	Class II	Class III	Class IV
$AlCl_3$	0.24	0.03	0.27	0.00	0.00	0.00
Al−F	0.20	0.05	0.00	0.25	0.02	0.00
Al−citrate	0.09	0.09	0.02	0.16	0.05	0.04
Al−oxalate	0.11	0.15	0.02	0.24	0.01	0.00
Al − fulvic acid	0.00	0.18	0.07	0.11	0.05	0.04
Al − litter leachate	0.02	0.15	0.10	0.07	0.03	0.00

(Table 1). Four reactivity classes of Al can be calculated from the results of the three measurements and the total Al in the system. Class I (Al_1) represents mainly monomeric Al in aquo- or hydroxo-complexes measured by the fast-oxine, pH 5.0 reaction, class II (Al_2-Al_1) the complex monomeric Al, and class III (Al_3-Al_2) the polymeric forms. Finally, class IV is the residual Al not measured by the slow-oxine, pH 8.3 reaction. The last could also be measured directly in natural waters by a method, such as graphite furnace atomic absorption spectrophotometry, that measures total dissolved Al.

Inorganic systems — The $AlCl_3$ system has an initial pH of 3.0, thus assuring that the dominant form of Al is Al^{3+}. The fast-oxine, pH 5.0 reaction complexes all of the Al in this system. Given that the dialysis time was limited to only 24 h to reduce errors caused by the adsorption of the Al on the membrane or walls of the container, the equilibrium between the interior and exterior of the tube was incomplete. Nonetheless the concentration inside the tube was about 90% of the original.

At pH 5.0, the original pH of the Al−F system, virtually all of the Al is in a fluoride complex. No Al was detected using the fast-oxine, pH 5.0 technique. Dialysis tubing does not separate the fluoride complexes from the monomeric aquo- and hydroxo-complexed Al; however, the Al−F complexes migrate through the dialysis tubing slightly more slowly than does Al^{3+}, as indicated by the value of 75% of the initial concentration found inside the tube. A small fraction (7%) of the Al in this system was measured as being in the polymeric form; it is uncertain whether the Al is really polymeric or whether some of the monomeric Al−F complexes were not extracted during the fast-oxine, pH 8.3 reaction.

Simple organic systems — One of the apparent characteristics of Al−organic complexes is that they have a broader range of bond strengths than do the inorganic complexes. The fast-oxine, pH 5.0 reaction extracts 0.02 mg Al/L from the Al−citrate system, while the fast-oxine, pH 8.3 reaction extracts an additional 0.16 mg/L. Together, classes I and II account for only 66% of the Al in the system; the rest is measured as being in the form of polymers or colloids. As expected, the dialysis tubing does not prevent the passage of these relatively small Al−organic complexes, although it does slow them down significantly, such that only about 33% as much Al is measured inside the tubing as in the original solution.

The results for the Al−oxalate system are similar to those of the Al−F system. Compared with the Al−citrate system, much less Al is found in classes III and IV as polymeric and colloidal forms. Again the dialysis tubing does not make any clear separation of these species.

Complex organic systems — The fast-oxine, pH 5.0 reaction is capable of extracting a significant amount of the Al from a system in which virtually all of the Al is originally in an Al−fulvic acid complex. Although 67% (18 mg/L) of the Al is measured as being monomeric (classes I and II), 26% was measured as being in class I. In contrast with the results of LaZerte (1984) a large proportion (33%) of the organically complexed Al was not extractable by the fast-oxine, pH 8.3 reaction. Unlike the fast-oxine, pH 5.0 reaction, the dialysis tubing makes a very good distinction between the inorganic and organically complexed forms of Al; no Al is measured in fraction A.

Although it is less certain that all of the added Al in the litter leachate system is organically complexed, in this case the contrast between the two methods is very clear. Whereas the dialysis method measures only 10% of the Al as being aquo- or hydroxo-complexes, the fast-oxine, pH 5.0 reaction measures 50%. The difference of 40% represents Al weakly bound to dissolved organic compounds that did not pass through the dialysis tubing. Again, quite a large amount of the added Al (15%) was not included in the measurement of monomeric forms.

The study shows that the oxine method separates the forms of Al by reactivity. Several cautionary notes should be added for those who wish to use the results presented here as a basis for interpreting analyses of natural waters. First, the concentrations of the complexing agents was much higher than in nature. Second, these were synthetic systems, each containing only one type of ligand, natural waters contain a large number of anions, including some that were not considered here such as SO_4 and SiO_5, that compete for the dissolved Al. The definition of the forms found in the reactivity classes is only approximate; as with the other common speciation procedures, these are operationally defined and not absolute.

Conclusions

(1) The speciation obtained using the fast-oxine, pH 5.0 method is not the same as that obtained using dialysis. In waters containing dissolved organic compounds capable of complexing Al, the fast-oxine, pH 5.0 method overestimates the amount of inorganic monomeric Al and thus causes an underestimation of the amount of organically complexed Al.

(2) Dialysis separates Al in large organic complexes from that present in ionic forms and in small complexes. However, the method does not distinguish between (a) weakly and strongly bonded Al in organic complexes or (b) the aquo- and hydroxo-complexes and the Al−F complexes.

(3) In the organic systems there were relatively large quantities of Al not extracted by the fast-oxine, pH 8.3 reaction; this suggests that the organic complexing agents cause a negative interference when oxine is used to determine Al.

(4) From one point of view the fast-oxine, low pH reaction

may be a better measure than dialysis of the toxicity of the Al in natural waters because it separates the forms by their reactivity. On the other hand, dialysis makes a clearer distinction between inorganic and organic forms. In the final analysis the merit of one or the other method in environmental studies will depend on its ability to predict the toxicity of the Al to aquatic life.

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Importance of Picoplankton in Lake Superior[1]

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In Lake Superior, approximately 50% of total primary production is attributable to phytoplankton that pass through a 3-μm screen. The <3-μm size class is dominated by eukaryotic flagellates, nonmotile eukaryotic cells (1 μm), and chroococcoid cyanobacteria. Approximately 20% of total primary production is attributable to orange autofluorescent chroococcoid cyanobacteria (mean size = 0.7 μm) as determined by size fractionation and track autoradiography. These small prokaryotes exhibited abundances of 42 000 and 56 000 $\mathrm{cells \cdot mL^{-1}}$, maximum photosynthetic rates of 7 and 6 $\mathrm{fg \cdot cell^{-1} \cdot h^{-1}}$, and growth rates of 1.5 and $0.8 \cdot \mathrm{d^{-1}}$ in the epilimnion and hypolimnion, respectively. A significant portion of this picoplankton (<1 μm) production may be consumed by heterotrophic protozoans in a "microbial loop."

Environ 50 % de la production primaire totale du lac Supérieur a pour origine des organismes phytoplanctoniques pouvant traverser un tamis à mailles de 3 μm. La classe de taille des <3 μm est dominée par des flagellés eucaryotiques, des cellules eucaryotiques non motiles (1 μm) et des cyanobactéries chroococcoïdes. La répartition selon les tailles et l'étude des tracés autoradiographiques a montré qu'environ 20 % de la production primaire totale était due à des cyanobactéries chroococcoïdes à autofluorescence orange (taille moyenne de 0,7 μm). Ces petits procaryotes présentaient respectivement, selon qu'ils se trouvaient dans l'épilimnion ou l'hypolimnion, des abondances de 42 000 ou 56 000 $\mathrm{cellules \cdot mL^{-1}}$, des taux maximums de photosynthèse de 7 et 6 $\mathrm{fg \cdot cellule^{-1} \cdot h^{-1}}$ et des taux de croissance de 1,5 ou $0{,}8 \cdot \mathrm{jour^{-1}}$. Une partie appréciable de la production de ce picoplancton (<1 μm) peut être consommée par des protozoaires hétérotrophes en « boucle microbienne ».

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Picoplankton (<1 μm) are important contributors to oceanic primary production (Li et al. 1983) and are usually dominated by chroococcoid cyanobacteria and small eukaryotes (Johnson and Sieburth 1979, 1982). The recognition of autotrophic picoplankton as an important part of the oceanic system has forced a reorganization of contemporary models of plankton dynamics, including both methodological impacts for primary production and theoretical impacts on pathways of carbon and energy flow (Sherr and Sherr 1984; Smith et al. 1984). However, the importance of picoplankton has not been determined in the upper Great Lakes, except for abundance estimates for phytoplankton <3 μm from Saginaw Bay (Sicko-Goad and Stoermer 1984). We investigated the abundance and production of <3- and <1-μm phytoplankton in Lake Superior and their possible role in the food web.

Methods

A 230-m-deep station in central Lake Superior (47°27′48″N, 88°34′42″W) was sampled 10 times between May 1 and October 15 in 1979 and once on September 28 in 1983.

Primary production was measured with the ^{14}C technique (Vollenweider 1974). In 1979, all incubations were carried out in situ for 4 h as described in Fahnenstiel and Glime (1983). In 1983, laboratory incubations were conducted for 1 h in 2-L polycarbonate bottles at 150 and 35 $\mathrm{\mu Ein \cdot m^{-2} \cdot s^{-1}}$. The higher light intensity is saturating for both epilimnetic and hypolimnetic phytoplankton in Lake Superior (G. L. Fahnenstiel, unpubl. data). After incubation, the contents of the incubation bottles were combined and split into several fractions. Whole water samples were filtered directly onto 0.45-μm Selectron membrane filters in 1979 and 0.22-μm Millipore filters in 1983. The remaining sample was fractionated by screening (3, 5, 10, 20, and 64 μm and 1, 3, and 10 μm were used in 1979

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[1] GLERL Contribution No. 439; GLRD Contribution No. 429.

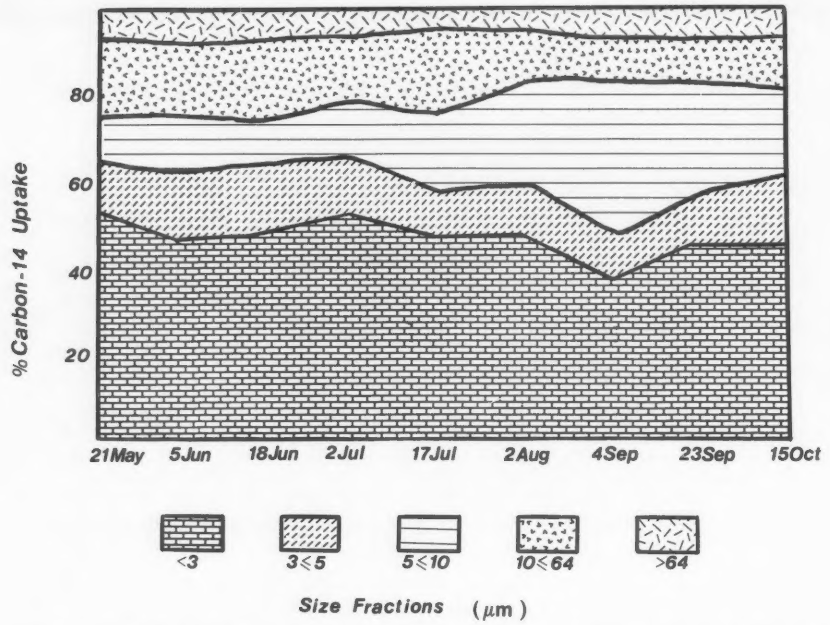

FIG. 1. Seasonal variation of ^{14}C fixation by percent contribution of various size classes in 1979 as determined by filter fractionation.

and 1983, respectively) and then final-filtering through 0.45-µm filters in 1979 and 0.22-µm filters in 1983. Nuclepore polycarbonate filters were used for the 1-, 3-, and 5-µm fractions and Nitex screens for the 10-, 20-, and 64-µm fractions.

In 1983, samples were also taken from the ^{14}C experiments and prepared for epifluorescence autoradiography (Fuhrman and Azam 1982). The remaining contents of the ^{14}C incubation bottles (whole and <1 µm) were preserved with either paraformaldehyde, glutaraldehyde, and sodium cacodylate (Lazinsky and Sicko-Goad 1979) or 1% formalin. Samples were in contact with the preservative for only a few seconds, at which time samples were filtered onto 0.22-µm Nuclepore filters. These filters were then inverted onto subbed cover slips (Fuhrman and Azam 1982) and dipped and developed for track autoradiography (Knoechel and Kalff 1976). Fading of autofluorescence can occur with prolonged storage and possibly during autoradiographic development. To minimize this fading we kept exposure time to a minimum (1−3 d) and performed replicate developments with and without the stop bath treatment. Some autofluorescent fading was noted relative to undeveloped samples, but this fading was not severe enough to cause significant problems. Loss of ^{14}C during the preservation, filtering, and autoradiographic preparation steps was monitored by filtration and did not exceed 10% with paraformaldehye and glutaraldehyde and 30% with 1% formalin. Number of tracks and cell size, shape, and color were noted for autofluorescent cells.

In 1979, phytoplankton samples were preserved with Lugol's solution and counted on an inverted microscope. In 1983, two sets of phytoplankton samples were taken. The first set was preserved and counted as in 1979. The second set was preserved with paraformaldehyde, glutaraldehyde, and sodium cacodylate for fluorescent and electron microscopy (Lazinksy and Sicko-Goad 1979). These preserved phytoplankton samples were stored on ice and returned to the laboratory for further processing. The TEM samples were concentrated by gentle centrifugation, rinsed four times in 0.1 mol cacodylate buffer$\cdot L^{-1}$ (pH 7.2), and then postfixed with 1% OsO_4 (osmic acid anhydride) in cacodylate buffer for 1 h at 4°C. The cells were then dehydrated in a graded ethanol and propylene oxide series and embedded in Epon (Luft 1961). Thin sections were cut with a diamond knife, collected on cleaned Formvar-coated 200-mesh copper grids, and stained with aqueous uranyl acetate (Watson 1958). Sections were examined with a JEOL JEM 100B electron microscope operating at 80 kV. Heterotrophic and autotrophic cells were counted on a Laborlux 12 microscope equipped for fluorescent microscopy (excitation 450−500 nm; emission >515 nm). Heterotrophic cells were also enumerated under light microscopy with a differential staining technique that consisted of imbedding 1-µm sections stained with toluidine blue-O (McCully et al. 1980).

Results

The 1979 results from three depths were averaged because vertical trends were not apparent (Fahnenstiel 1980). The <3-µm size class accounted for 40−54% (mean = 47%) of the total carbon fixed, while the <10-µm size class accounted for 78% (Fig. 1). Few seasonal trends were found in any size class. The 5- to 10-µm size class appeared to fix more carbon during the thermally stratified period (August−September) when there was a rapid increase in the diatom *Cyclotella* (Fahnenstiel and Glime 1983).

In 1983, the <3-µm size class was studied in more detail. Since little seasonal variability was found in 1979, only one period was sampled in 1983. The amount of carbon fixed in the <3- and <10-µm size classes was similar to measurements in 1979, and the <1-µm size class accounted for approximately 20% of the total carbon fixed. Following are the percentages of

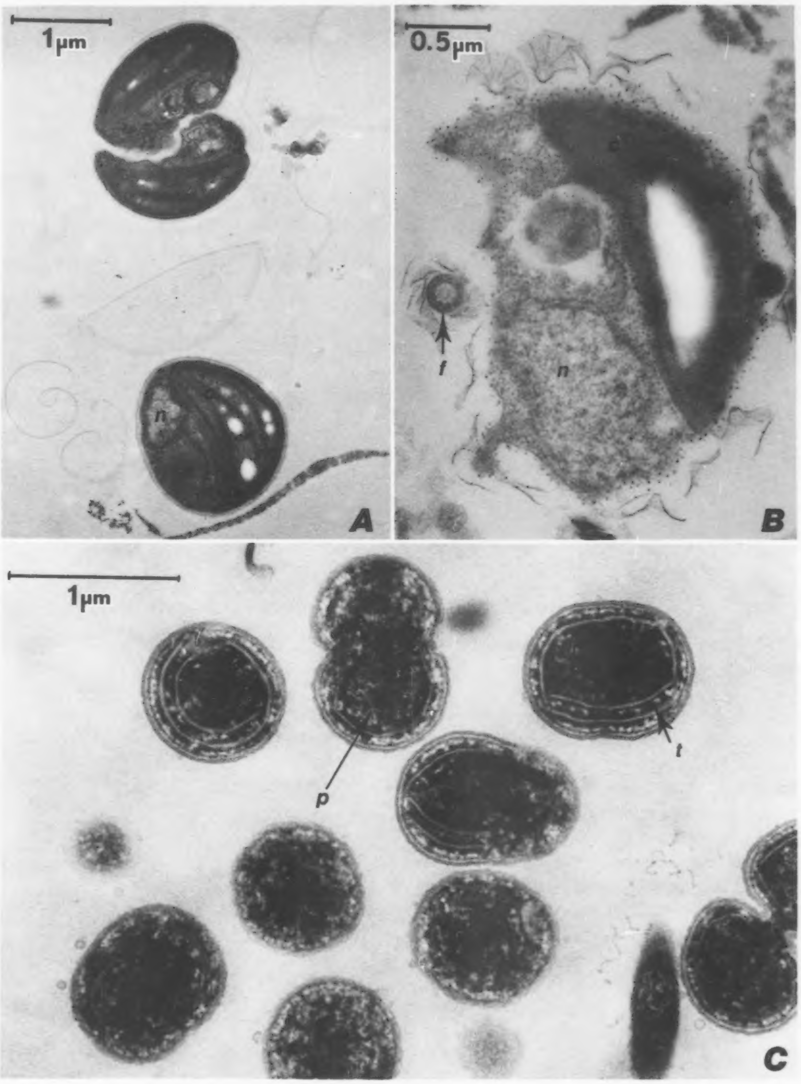

FIG. 2. Transmission electron micrographs of Lake Superior picoplankton (A) Eukaryotic green cell. This tiny nonflagellated phototroph has visible chloroplast (c) and nucleus (n). (B) Eukaryotic microflagellate. This small flagellate has visible nucleus, chloroplast, and flagella (f), with scales on cell and flagella. (C) Orange autofluorescent chroococcoid cyanobacteria. These small prokaryotes have polyhedral bodies (p) and peripheral arrangement of thylakoids (t), which are separated by dense cytoplasmic material.

total carbon fixed in the <1-, <3-, and <10-μm size fractions in 1979 and 1983:

	1979 (yearly average)	1983 (September)
<1	—	20
<3	47	49
<10	78	76

The predominant organisms in the 1- to 3-μm size category were green eukaryotic cells, cyanobacteria, and small flagellates, while the predominant organisms in the <1-μm size class were small (range = 0.4−1.0 μm; mean = 0.7 μm) orange autofluorescent chroococcoid cyanobacteria (Fig. 2; Table 1). The orange autofluorescent color of these cyanobacteria when excited with blue light indicates the presence of phycoerythrin (Waterbury et al. 1979). These chroococcoid cyanobacteria were present at abundances of 42 000 and 56 000 cells·mL^{-1} and exhibited light-saturated carbon fixation rates of 7 and 6 fg.·cell^{-1}·h^{-1} for samples from the epilimnion and hypolimnion, respectively. Approximately 77 and 91% of the carbon fixed in the <1-μm size class from the epilimnion and hypolimnion, respectively, were fixed by these

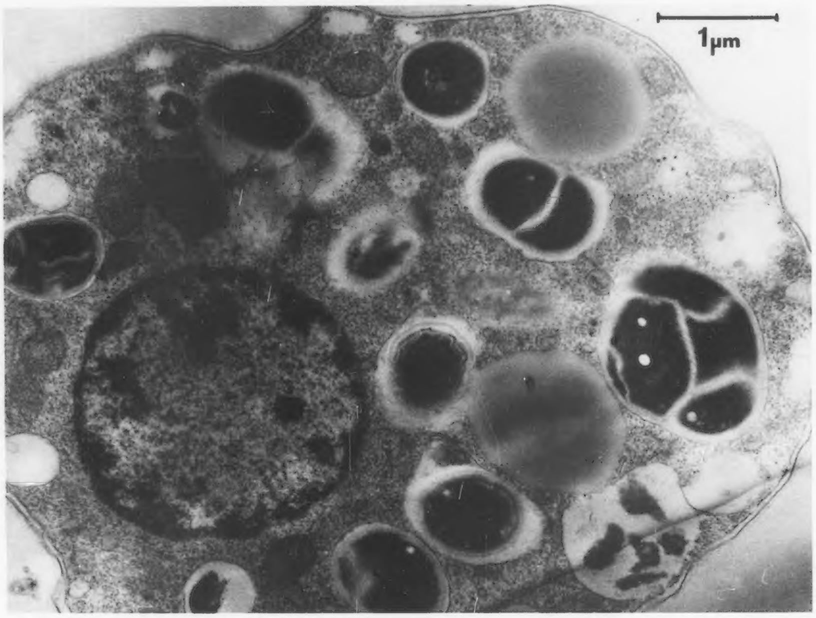

FIG. 3. Transmission electron micrograph of heterotrophic protozoan in Lake Superior. This protozoan has ingested many cyanobacteria (cb) which can be seen in food vacuoles.

small prokaryotes. Since 20% of these cyanobacteria were removed by 1-μm fractionation (Table 1), total cyanobacteria production was calculated by multiplying cyanobacteria abundance and specific production rate. Thus, cyanobacteria were responsible for 16–24% of the total primary production (Table 1). Growth rates for cyanobacteria were calculated from carbon fixation expressed on a daily basis and an estimate of their carbon content. The 1-h photosynthetic rates were converted to daily rates based on typical incident and depth-attenuated light intensity using the numerical model of Fee (1973). Carbon content was determined from average cell volume assuming 121×10^{15} μg $C \cdot \mu m^{-3}$ (Watson et al. 1977). The calculated exponential growth rates for these cyanobacteria were $1.5 \cdot d^{-1}$ in the epilimnion and $0.8 \cdot d^{-1}$ in the hypolimnion.

Electron microscopy performed in 1983 revealed abundant heterotrophic protozoans in the 3- to 20-μm size range (Fig. 3). The term heterotrophic protozoans refers to microheterotrophs (<20 μm), which are flagellated, ciliated, and ameboid organisms. Preliminary abundance estimates from epifluorescent and differential stained counts for these protozoans are in the range of 400–500 $cells \cdot mL^{-1}$, with an estimated biomass of 49–60 $mg \cdot m^{-3}$ and carbon content of 7.35–9 mg $C \cdot m^{-3}$. Many of these protozoans from both epilimnetic and hypolimnetic samples had ingested cyanobacteria, as can be seen in Fig. 3 where approximately 10 cyanobacteria (some partially digested) are contained in food vacuoles of a protozoan.

TABLE 1. Abundance and primary production of chroococcoid cyanobacteria in the epilimnion and hypolimnion of Lake Superior in September 1983.

	Epilimnion	Hypolimnion
Total autofluorescent cells ($cells \cdot mL^{-1}$)	44 001	60 799
Chroococcoid cyanobacteria ($cells \cdot mL^{-1}$)	40 471	54 312
Chroococoid Cyanobacteria in <1-μm size fraction ($cells \cdot mL^{-1}$)	34 214	41 504
Maximum primary production rate[a] ($fg\ C \cdot cell^{-1} \cdot h^{-1}$)	7	6
Exponential growth rate[a] (d^{-1})	1.5	0.8
Primary production in <1-μm size fraction[b] ($\mu g\ C \cdot L^{-1} \cdot h^{-1}$)	0.31	0.27
Calculated cyanobacteria production in <1-μm size fraction (abundance × production[a] = $\mu g\ C \cdot L^{-1} \cdot h^{-1}$)	0.24	0.25
Total cyanobacteria production (abundance × production[a] = $\mu g\ C \cdot L^{-1} \cdot h^{-1}$)	0.28	0.30
Percent of total primary production attributable to cyanobacteria	16	24

[a] Determined by track autoradiography.
[b] Determined by filter fractionation.

Discussion

Small phytoplankton are an important part of the Lake Superior ecosystem. Phytoplankton that passed through 3- and 1-μm screens were responsible for 48 and 20% of the primary production, respectively. Their importance appears to be a consistent feature of Lake Superior, since little seasonal or yearly variability was found. Our work is also consistent with that of Munawar et al. (1978), who found that phytoplankton <5 μm were the major primary producers in Lake Superior.

Fractionation experiments are relatively easy to perform, but can often be difficult to interpret without microscopic analysis of fractionated size classes (Runge and Ohman 1982). We examined the components of <3- and <1-μm size classes by light, fluorescent, and electron microscopy after they had been fractionated. The <3-μm size class was dominated by microflagellates, eukaryotic green cells, and cyanobacteria (Fig. 2). The composition of this size class is very similar to that found in certain oceanic plankton communities (Johnson and Sieburth 1982). Chroococcoid cyanobacteria (mean size = 0.7 μm) dominated the <1-μm size class. Similar cyanobacteria were found in Lake Ontario (Caron et al. 1985) and in Grand Traverse Bay of Lake Michigan (Sicko-Goad and Stoermer 1984), suggesting that cyanobacteria may be a ubiquitous part of the Great Lakes ecosystem. In Lake Superior, these small organisms were responsible for 16–24% of the total primary production and exhibited relatively fast growth rates of 1.5 and $0.8 \cdot d^{-1}$ in the epilimnion and hypolimnion, respectively. Landry et al. (1984) found comparable growth rates of $1.4-1.7 \cdot d^{-1}$ for cyanobacteria at stations off Hawaii. The cyanobacteria from Lake Superior probably belong to the genus *Synechococcus*, since they are morphologically similar to those described as Type 1 by Johnson and Sieburth (1979).

The exact role of these small cyanobacteria in the Lake Superior food web is still uncertain; inevitably some portion of this production must be consumed directly. However, Lake Superior's zooplankton community is dominated by calanoid copepods (Watson and Wilson 1978), which are unable to effectively graze particles of this size (Vanderploeg 1981; Johnson et al. 1982). We believe that a sizeable fraction of picoplankton production is consumed by heterotrophic protozoans. We found considerable evidence that protozoans can ingest cyanobacteria in Lake Superior (i.e. Fig. 3). Although our evidence is primarily for ingestion, Johnson et al. (1982) found that two microheterotrophs could use and subsist on similar sized cyanobacteria. Furthermore, heterotrophic protozoans are a common part of the Lake Superior plankton community. Munawar and Munawar (1978) found Lake Superior to be dominated by flagellates, many of which are heterotrophs (e.g. *Katablepharis*, *Cryptaulax*, and some *Ochromonas* spp.). Our preliminary estimates of protozoan (flagellates and nonflagellates) abundance are $400-500$ cells$\cdot$mL^{-1}. If we assume that these protozoans have a maximum filtering rate of 1.9 L$\cdot$cell$^{-1} \cdot d^{-1}$ (Fenchel 1982), we can expect a maximum loss rate of $0.76-0.95 \cdot d^{-1}$. This loss rate would be a significant fraction of the cyanobacteria growth rate and suggests that protozoans may be significant grazers of cyanobacteria.

Our evidence for the importance of protozoans in grazing chroococcoid cyanobacteria in Lake Superior is not very complete; however, our contention has support from work in other aquatic environments. In many marine systems, protozoans are an important link in the food web as part of the so-called "microbial loop" (Azam et al. 1983). Heterotrophic protozoans provide the link between small producers and larger multicellular zooplankton (Haas and Webb 1979; Linley et al. 1983; Sherr and Sherr 1984). This same link may also be an important part of the Lake Superior food web. Since approximately 20% of the primary production originates in phyoplankton that are not readily consumed by copepods, protozoans in the 3- to 20-μm range may be important in passing this production to the "classical" food web. Conventional thought regarding carbon and nutrient cycling would be profoundly affected by this "microbial loop" (Sherr and Sherr 1984).

Much more work is needed to confirm this hypothesis, but our results clearly indicate the importance of chroococcoid cyanobacteria and their ingestion by protozoans.

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Sports Angler Preferences for Alternative Regulatory Methods

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Renyard, T. S., and R. Hilborn. 1986. Sports angler preferences for alternative regulatory methods. Can. J. Fish. Aquat. Sci. 43: 240–242.

Successful implementation of fisheries regulations is difficult when user groups strongly oppose the regulations. We show that some types of sports fishing regulations (seasonal closure, daily bag limits) are not generally acceptable to British Columbia salmon sports anglers and that preference for other regulations depends upon the frequency of fishing. Infrequent anglers prefer low annual bag limits, while frequent anglers prefer larger size limits and gear restrictions.

Il est difficile de mettre efficacement en application les règlements sur les pêches quand des groupes d'utilisateurs s'y opposent énergiquement. Nous faisons ressortir que les pêcheurs sportifs de saumon de la Colombie-Britannique n'acceptent pas, de façon générale, certains types de règlements (période d'interdiction saisonnière, limites des prises journalières) et que la préférence démontrée pour d'autres règlements dépend de la fréquence avec laquelle on pêche. Les pêcheurs occasionnels préfèrent des limites de prises annuelles réduites tandis que ceux qui pêchent souvent préfèrent qu'on impose des limites de taille plus élevées et des restrictions sur les engins de pêche.

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Much research has been conducted on the motivations, needs, and preferences of anglers in regard to the fishing experience (Carl 1982; Hudgens 1984; Knopf et al. 1973; Moeller and Engelken 1972; Smith 1980; Leedy et al. 1981). Evaluation of the needs, preferences, and motivations of the angler have been thought necessary for responsible agencies in shaping a management plan that is sensitive to the people it affects (Duttweiler 1976; Smith 1980). Thus, motivations for fishing that contribute to an increase or decrease in catch and effort have been considered important to assess the impact of various regulatory options (Smith 1980). This requires, however, considerable social research. An alternative is to ignore motivations and look directly at regulatory preferences in relation to fishing behavior.

A recent trend in Pacific salmon sport fisheries management is to give anglers a larger voice in regulatory decision-making. In the United States, this takes the form of representatives on regional management councils and similar state bodies such as the Board of Fisheries in Alaska. In Canada, it is less formal but does occur through Ministerial advisory boards.

Councils and advisory boards have given anglers a voice, but this has led to other problems. First, these formal decision-making processes have been hampered by endless public meetings and political lobbying. Hilborn et al. (1984), for instance, described a set of sports fishing regulations that were introduced by the Department of Fisheries and Oceans (DFO) to manage the salmon sport fishery and were stopped by strong political lobbying by the Sports Fishery Advisory Board. This process usually does not make it clear to managers whether a

TABLE 1. Comparison of infrequent and frequent fishermen responses of the (a) most preferred and (b) least preferred regulation using the number of trips made per year as the effort variable. Expected values (in parentheses) were calculated on the assumption that there are no differences between groups ($N = 144$; df = 6).

	(a) Most preferred ($G = 25.947$, $\alpha = 0.0002$)			(b) Least preferred ($G = 8.877$, $\alpha = 0.1806$)		
Regulation	Count	≤20 trips	>20 trips	Count	≤20 trips	>20 trips
Winter closure	8	5 (4)	3 (4)	43	17 (20)	26 (23)
Summer closure	16	1 (8)	15 (8)	40	19 (19)	21 (21)
Yearly bag	61	38 (29)	23 (32)	4	2 (2)	2 (2)
Size limits	24	9 (11)	15 (13)	5	5 (2)	0 (3)
Daily bag	4	1 (2)	3 (2)	32	15 (15)	17 (17)
Gear restriction	25	9 (12)	16 (13)	5	3 (2)	2 (3)
Annual harvest	6	5 (3)	1 (3)	15	7 (7)	8 (8)
Missing	6	4	2	6	4	2
Total	150	68	76	150	68	76

more acceptable regulation package could be found that would achieve the same management objective. Second, it is not clear whether opinions expressed by the individuals in councils and advisory boards represent all anglers. Government advisory bodies are typically composed of a nonrandom sample of the interest group; according to political theory (Olson 1975; Moe 1980), only those individuals or firms who are large will reap significant benefits from their own involvement. Thus, commercial resort owners, club and organization officers, and very active sport anglers can expect to participate in advisory groups. How do fishery managers get advice that represents the opinion of the majority of anglers?

We propose that a survey of anglers is a more direct tool for managers to get angler preferences for regulation. Our proposal follows the rationale of other authors who have found, in other circumstances, that the questionnaire is a reliable and systematic method (Babbie, 1973; Duttweiler 1976).

Hypothesis of Angler Preferences

Our general hypothesis is that anglers will prefer regulations that least affect their fishing behavior. Specifically, we hypothesize that frequent or efficient anglers would not prefer an annual or daily bag limit because they will often exceed these limitations if left unrestricted. The frequent/efficient angler would prefer increased size limits and gear restrictions, since his catch would not be substantially reduced because of his superior abilities. We hypothesize that the infrequent or inefficient angler, on the other hand, would prefer bag limits because he often does not achieve the maximum allowable catch. In addition, an infrequent/inefficient angler would not prefer gear restrictions or increased size limits because restrictions on the few fish he catches and the few techniques he uses will disrupt his fishing experience.

Materials and Methods

We surveyed 157 British Columbia sport anglers between December 6, 1983, and January 15, 1984, at the Burrard Civic and Horseshoe Bay marinas (Vancouver and Horseshoe Bay, British Columbia) for their trip frequency, annual success, and regulation preferences. About 95% of the anglers were interviewed on weekend days and 5% on weekdays. We interviewed between 10:30 a.m. and 3:00 p.m. when marinas were most crowded with anglers. We considered anyone with a current B.C. Tidalwater Sport Fishing License as an eligible interviewee. About 90% of the anglers had just finished fishing, 5% were just starting to fish, and 5% were just observing incoming catches. Six anglers interviewed did not complete the survey and seven refused to answer any questions.

We asked each angler four questions. The first two questions established the number of trips taken and the number of salmon caught in 12 mo. The remaining two questions required that each respondent select his most preferred and least preferred regulations from a list of seven.

The seven alternative regulations that are assumed to have the same conservation effect on the chinook and coho stocks in the Strait of Georgia are (1) a winter closure from October through June every year, (2) a summer closure from June through July every year, (3) an annual bag limit of 20 salmon per year, (4) an increase in the legal size limits for coho (12 to 20 in. (305 to 508 mm)) and chinook (18 to 24 in. (457 to 610 mm)), (5) a decrease in the daily bag limit from four to one, (6) gear restrictions including the banning of downriggers, barbed hooks, and multiple hooks, and (7) an annual harvest restriction of 150 000 chinook and 500 000 coho for the sport anglers as a collective group (Argue et al. 1983; T. Shardlow, DFO, 60 Front Street, Nanaimo, B.C., pers. comm.).

The original questionnaire was pretested on 10 anglers after some initial revision. The pretest was used to determine the clarity of the questions and whether or not it produced the desired responses. The pretest identified three problems. First, the survey took too long to complete because anglers were often cold and anxious to pack up for home. We felt that shortening the survey to four questions (from nine) and by requiring the anglers to rank only two of seven choices ensured the completion of more surveys. Second, the first two questions required the angler to estimate the fishing trips taken and salmon caught over the last 12 mo. However, whether we used "over the last 12 mo" or "last year" as the wording to the questions, there was confusion. We chose to explain, during each interview, that each angler consider the 12-mo period prior to the survey day. Third, most anglers expressed confusion about the "annual harvest" regulation. This option required further explanation during the interview. This option was retained because once each angler was informed as to the overall estimated reduction in catch (from 100 000 to 80 000 for chinook and from 400 000 to 320 000 for coho), they were able to make an informed judgement about the regulation.

We defined a frequent angler as one who fished more than

20 times per year and infrequent as less than 20 times. Similarly, we defined an efficient angler as one who caught more than 20 salmon per year and inefficient as less than 20. This split our sample by putting approximately half of the anglers in each category. Thus, we stratified our sample into groups based on frequency of fishing (≤20 times per year or >20 times per year), total catch (≤20 fish per year or >20 fish per year), and daily success rate (≤1 fish per day or >1 fish per day). Hilborn (1985) has shown that the major determinant of sport fishing annual catch is the amount of time spent fishing and not individual efficiencies; this strong correlation between trip frequency and annual catch, both in Hilborn's (1985) and in our sample, led us to restrict our analysis to trip frequency.

Results and Discussion

The most preferred regulation by all anglers was the annual bag limit of 20 salmon (Table 1). Although infrequent anglers preferred this regulation more than expected and frequent anglers less than expected, it is possible that some of the preference for this regulation is due to similarity of this choice to the present regulation. The current regulation is 30 chinook salmon per year with no annual bag limit on coho salmon. Some interest was shown by frequent anglers on the summer closure, size limits, and gear restrictions; little preference was shown by infrequent anglers regarding regulations other than annual bag limit (Table 1a). All anglers sampled least preferred winter or summer closure and the daily bag limit (Table 1b). Yearly bag limits, size limits, and gear restrictions were rarely selected as the least preferred regulation (Table 1b). The data show, therefore, that all anglers have similar "least preferred" regulations but have different "most preferred" regulations.

Time closures were generally found unpopular. However, frequent anglers selected the summer closure more often than infrequent anglers as a preferred regulation. This seems contrary to the logic that restricted time would affect the frequent angler more. T. Shardlow (DFO, 60 Front Street, Nanaimo, B.C., pers. comm.) found in a similar survey during the summer of 1983 that there was a high preference for the winter closure. This suggests that there may be two major subgroups within the sport fishing community, one that prefers winter fishing and another that prefers summer fishing. Our data suggest that frequent anglers fish more in winter.

Our sample is not likely to represent the proportion of anglers in each frequency category because it was a small survey, restricted to a few marinas and limited to a short period. We feel, however, that it is important to decision-makers to know the wide distribution of the opinions expressed in our sample. To determine more reliable province-wide estimates, we derived proportions from the data recently collected in the DFO logbook program (Bijsterveld 1983). The logbook program randomly selected about 2000 anglers from sport license records and is more likely representative of the proportion of British Columbia sport anglers in the frequency categories. The logbook data show that 82% (or 213 900 province-wide) are infrequent anglers and 18% (or 48 300) are frequent anglers. Therefore, the opinions expressed by the infrequent anglers in our sample represent a large majority of the sport anglers of British Columbia.

One would expect, then, that if the Sport Fishery Advisory Board and DFO had all sport angler interests in mind, they would choose regulations that affect fewer anglers. For example, a regulation package in the interest of many anglers would include (1) a smaller annual bag limit, (2) no change in gear restrictions or size limits, (3) no time closures, and (4) no reduction in daily bag limits.

The current decision-making process is susceptible to the biases, whether intentional or not, of frequent anglers. The Sport Fishery Advisory Board members and fishery managers are likely avid, frequent anglers who have much at stake in the sport fishery. Surveys such as the one we have considered are one method to safeguard against the biases of decision-makers. Our hypothesis, for instance, provides a good example of manager bias. Our original hypothesis stated that frequent anglers prefer one type of regulation, while infrequent anglers prefer others. Our survey, instead, found some regulations that were disliked by all anglers, while some preference variation occurred for "most preferred" regulations. User preference surveys clarify the position of all anglers regarding the acceptability of alternative policies, and may become a major tool in fisheries management.

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Acclimation-Induced Change in Toxicity of Aluminum to Rainbow Trout (*Salmo gairdneri*)

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When a group of rainbow trout (*Salmo gairdneri*) fingerlings was exposed to 87 μg Al/L for 1 and 2 wk, their threshold lethal concentration (LC50) increased to about 1.8 times the control LC50 of 175 μg Al/L. Raising sublethal exposure to 154 μg/L during the third week resulted in a similar ratio of 1.7 between LC50s of previously exposed and control fish. Thus, prior exposures of 0.5 and 0.9 of the control LC50 resulted in about the same increase in tolerance. The magnitude of the increase was similar to those reported in the literature for other metals. Such acclimation could assist in the survival of fish during spring and autumn surges of aluminum and other metals in surface waters acidified by atmospheric deposition of oxides of sulfur and nitrogen; those environmental changes in aluminum concentration parallel the concentrations used in this research. Experimental water simulated an acid lake with pH of 5.1–5.3 and total hardness of 11 mg/L.

L'exposition, pendant 1 ou 2 sem, d'un groupe d'alevins non vésiculés de truite arc-en-ciel (*Salmo gairdneri*) à une concentration d'aluminium de 87 μg/L s'est traduite par une augmentation du seuil de la concentration létale (CL_{50}) d'environ 1,8 fois par rapport aux témoins (175 μg Al/L). La concentration sublétale a été portée à 154 μg/L pendant une troisième semaine d'exposition et le rapport des CL_{50} des poissons déjà exposés et des témoins est demeuré semblable (1,7). Des expositions antérieures à 0,5 et 0,9 fois la CL_{50} des témoins se traduisaient donc par une augmentation semblable de la tolérance. Cette augmentation est du même ordre que celle signalée dans les publications pour d'autres métaux. Une telle acclimatation pourrait favoriser la survie des poissons pendant les montées soudaines, au printemps et à l'automne, des concentrations d'aluminium et d'autres métaux dans les eaux de surface acidifiées par le dépôt atmosphérique d'oxydes de soufre et d'azote. Les concentrations d'aluminium utilisées pour la présente étude sont du même ordre que celles notées dans le milieu naturel. L'eau utilisée pour l'étude simulait celle d'un lac acide de pH 5,1–5,3 et de dureté totale de 11 mg/L.

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Recent work has demonstrated that fish can increase their tolerance of certain metals if they have been previously exposed to a sublethal level of that metal (copper, Dixon and Sprague 1981b; Buckley et al. 1982; McCarter and Roch 1983, 1984; cadmium, Duncan and Klaverkamp 1983; zinc, Bradley and Sprague 1985; and mixtures, Roch and McCarter 1984a). If there were such acclimation to aluminum, it could be significant for survival of fish in waters which are being acidified by atmospheric fallout. Aluminum is one of the metals which increases in concentration in acid lakes and makes a major contribution to toxicity (Schofield and Trojnar 1980; Hutchinson 1984). It is present at sublethal levels during the early stages of acidification of most susceptible lakes (Hutchinson 1984), providing a potential stimulus for acclimation. Increased tolerance might allow fish to survive the dramatic surges in metal concentration which occur during snowmelt and autumn runoff (Driscoll et al. 1980; Schofield and Trojnar 1980).

The present study was designed to show whether fish acclimate to aluminum, as judged by an increase in their tolerance of the metal, and if so, the general magnitude of any change in tolerance. It tested the null hypothesis that prior exposure of trout to a sublethal concentration of aluminum ("pre-exposure") would not alter the lethal threshold of the metal.

The study also intended to show whether a very high level of pre-exposure would elicit a stronger acclimation response than an intermediate pre-exposure. Previous research with copper indicated that the increase in tolerance was proportional to the strength of prior exposure, within limits; pre-exposure to at least 0.18 of the LC50 was required to trigger an increase in tolerance, but there was a "plateau" for maximum increase in tolerance for a pre-exposure range from about 0.4 LC50 up to at least 0.6 LC50 (Dixon and Sprague 1981b). Accordingly, pre-exposures of 0.5 and 0.9 of a control LC50 were used in the present study to test the null hypothesis that there would be no difference between the subsequent tolerances (=incipient lethal levels or threshold LC50s, Fry 1971).

Methods

Procedures were those previously established in our laboratory for work on acclimation, and the descriptions in Dixon and Sprague (1981a, 1981b) are applicable for details of tank sizes, flow rates, fish source, feeding regimes, etc. An outline of the general protocol is repeated here, along with a description of items specific to this experiment.

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Rainbow trout (*Salmo gairdneri*) of 3.5 g initial wet weight were held in flowing experimental water for 4 wk. Trout were then split into two groups of 300 and held in pre-exposure tanks for a further week. Aluminum at 87 μg/L was then started in one pre-exposure tank (day 0) and maintained until day 14; the other pre-exposure tank was the control. On day 14 the aluminum concentration was increased to 154 μg/L for pre-exposed fish. It was necessary to attain the higher pre-exposure level in two stages because preliminary experiments demonstrated that sudden exposure of naive trout to that level caused about 15% mortality.

Lethal tests were initiated on days 0, 7, 14, and 21 using samples of fish collected just before any change in pre-exposure level. There were 10 pre-exposed fish at each of six test concentrations including zero. Control fish that had no prior exposure to Al were tested simultaneously. The flow of test water at a given concentration was split between a test tank of pre-exposed fish and one of control fish to maintain identical conditions and avoid discrepancies of analysis. Randomization of fish and tanks was practised throughout. There was no mortality of fish in zero concentrations of the lethal tests, and mortality during pre-exposure was less than 1%. Each lethal test continued for 6 d and threshold or incipient lethal levels were established in 5 d or less. The 120-h LC50s were estimated by a computerized trimmed Spearman−Karber method (Hamilton et al. 1977), and statistical differences between pairs of LC50s were assessed by standard error of the difference using $P < 0.05$ as a criterion.

The soft water was derived from well water by reverse osmosis and from the university deionized supply, both run through ion-exchange columns. This was followed by the addition of 3.4% of the same hard well water to provide a mix of natural ions. Its quality during holding, pre-exposure, and testing was similar with total hardness 11.2 mg/L as $CaCO_3$ (SD = 4.0, $N = 65$), temperature 15°C (SD = 0.6, $N = 158$), and dissolved oxygen 9.0 mg/L (SD = 0.5, $N = 55$) or greater than 85% saturation. Scans of three samples of control water by inductively coupled plasma emission gave the following average values (milligrams per litre): Na, 9.3; Ca, 2.9; Mg, 1.1; Si, 0.6; K, <1; P, <0.5; B, 0.009; and (micrograms per litre): Pb and Zn, less than the detection limit of 50; Al, Cd, Cr, Fe, and Mn, <10; Cu, <8. The experimental water was acidified by an automatic titrating unit dispersing dilute H_2SO_4. During pre-exposure, pH averaged 5.25 (SD = 0.21, $N = 44$). The pH values in test tanks for control and pre-exposed fish were nearly identical but they varied slightly among the four successive lethal tests, averaging 5.22 (SD = 0.16), 5.31 (SD = 0.17), 5.09 (SD = 0.15), and 5.18 (SD = 0.09) with $N \geq 80$ in each case. The experimental pH not only simulated an acid lake, but yielded maximal toxicity of aluminum, and minimal changes of aluminum from one chemical form to another.

Stocks solutions of aluminum contained reagent grade $Al_2(SO_4)_3 \cdot 18H_2O$, deionized water, and H_2SO_4 to lower pH to 2.8−3.6 as required to achieve the desired pH in test tanks (the aluminum salt itself had some acidifying effect). Average measured concentrations of total aluminum are used throughout this paper, based on seven samples during pre-exposure and two to four samples for each concentration of each lethal test. Samples were acidified to pH < 2.0. Precision of analysis by flameless AAS was good, judging by the average coefficient of variation of 5.4% on five triplicate samples submitted without the knowledge of the analyst. Measured test concentrations averaged 120% of nominal values but results for each test concentration were relatively constant, with an average coefficient of variation of 6.6% through the four lethal tests, scarcely greater than the analytical variation.

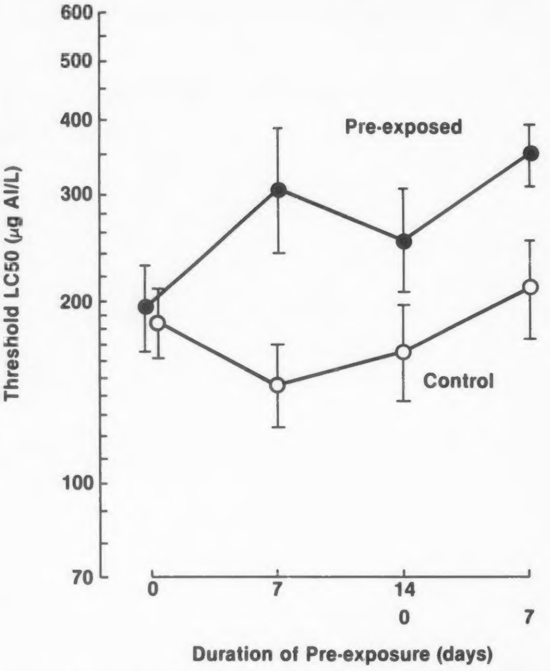

FIG. 1. Changed tolerance of aluminum in rainbow trout pre-exposed to sublethal levels of the metal. The pre-exposed fish were held in 87 μg Al/L for 14 d and then in 154 μg/L for a further 7 d. Control fish were held in <6 μg/L. Total hardness of experimental water averaged 11 mg/L as $CaCO_3$, and pH averages were 5.1−5.3. The 95% confidence limits of the LC50s are shown.

Results

Control LC50s showed some variation (Fig. 1) but the geometric average of the four LC50s determined for unexposed fish at different times was 175 μg/L, very close to the day 0 mean value of 189 μg/L. Thus, the initial 2-wk pre-exposure to 87 μg/L may be considered to represent 0.50 of the control LC50, and the final week of exposure to 154 μg/L represented 0.88 of the control LC50.

After 7 d of pre-exposure, fish had increased their LC50 to 2.1 times that of control fish tested at the same time, and after 14 d the ratio was 1.5 times (Fig. 1). Differences between control and pre-exposure LC50s were statistically significant on each day. An average ratio of 1.8 might be taken to represent the increase in tolerance of aluminum following pre-exposure to 0.50 LC50 (see Discussion). On day 21, after increasing the acclimation concentration, pre-exposed fish were 1.7 times more tolerant than controls, again a significant difference.

Pre-exposed fish did not differ in size from control fish. The trout grew during holding and experimental periods to about 5.5 g on day 0 and 7.9 g on day 21. No statistical difference was demonstrated in wet weights or lengths of pre-exposed fish compared with control fish (three-way ANOVA). Mean wet weights (grams) of pre-exposed trout (control trout in parentheses) used in tests were as follows: day 0, 5.2 (5.8); day 7, 5.9 (6.0); day 14, 6.3 (6.6); day 21, 7.8 (8.0). Coefficients of variation averaged 29%.

Discussion

The tolerances of aluminum shown by pre-exposed fish were significantly higher than those of control fish and the first null hypothesis is therefore rejected. We conclude that a 1- or 2-wk exposure of rainbow trout to half the lethal level of aluminum results in increased tolerance by a factor in the vicinity of 1.5–2.1, or approximately 1.8-fold.

At 21 d, after increasing the aluminum acclimation concentration, the tolerance ratio of pre-exposed to control fish was similar, at 1.7. We do not consider that our results demonstrate any change in degree of acclimation from 7 to 21 d, either with duration of pre-exposure or with level of pre-exposure. There is within-test variability associated with each LC50 determination as indicated by the confidence limits in Fig. 1, and slight changes of LC50s in opposite directions could greatly alter the ratios. The small drift in control LC50s might be related to change in aluminum toxicity at slightly different test pHs, but in fact such differences, or greater ones, are usual in repeated tests within a laboratory (Sprague 1984). There are no grounds for rejecting the second null hypothesis, and we conclude that pre-exposure to 0.9 LC50 or 0.5 LC50 results in the same degree of increased tolerance. It appears that the "plateau" of maximum increase in tolerance, found for pre-exposures to copper of 0.4–0.6 LC50 by Dixon and Sprague (1981b), may apply to other metals such as aluminum and extend upwards to 0.9 LC50.

Most other values in the literature for lethal levels of aluminum for fish tend to be higher than our control values. Near-threshold LC50s for brook trout (*Salvelinus fontinalis*) fry would be about 420 μg Al/L at pH 5.2 and hardness 5 mg/L (Driscoll et al. 1980), or in the vicinity of 350 μg Al/L judging from data of Schofield and Trojnar (1980), also at pH 5.2. Brook trout fingerlings were reported to show 4-d LC50s of 380 μg Al/L at pH 5.6 and hardness 2 mg/L and 3000 μg Al/L at the same pH and hardness 18 mg/L (Tandjung et al. 1982). At alkaline pH, which would involve major changes in speciation of aluminum, LC50s for rainbow trout are in the thousands of micrograms of total aluminum per litre (Freeman and Everhart 1971).

The pre-exposure to aluminum apparently did not affect growth of trout. Any metabolic cost of activating defence mechanisms must have been small. In similar experiments showing acclimation to copper, growth was reduced for pre-exposure of 0.29 LC50 and higher (Dixon and Sprague 1981b; Buckley et al. 1982). Growth differences could, of course, be the result of changes in appetite and food consumption (e.g. Freeman and Everhart 1971), food conversion efficiency, or activity.

These findings could have relevance for fish in acidified surface waters, in which total aluminum levels of 20–320 μg/L have been reported from the U.S. Adirondacks, 20–600 μg/L from southern Norway, and 190–200 μg/L in Sudbury lakes of Canada (Schofield and Trojnar 1980; Wright et al. 1980; Gunn and Keller 1980). Some of this aluminum forms complexes with inorganic ions, and much of it may be bound by organic ligands and be practically nontoxic (Driscoll et al. 1980; Baker and Schofield 1982). Nevertheless, labile inorganic aluminum in acidified creeks may increase from 50–150 μg/L during much of the year to 200–300 μg/L during spring and autumn runoff (Driscoll et al. 1980) (i.e. the same ranges of "pre-exposures" and LC50s that are reported in the present experiment). The modest degree of acclimation shown by the trout might therefore be of significance in surviving spring and autumn surges of aluminum, along with other metals. Zinc and copper are the two other toxic metals which are mobilized and are therefore important in waters undergoing acidification (Hutchinson 1984) and to which fish can also acclimate (Chapman 1978; Dixon and Sprague 1981b; Bradley and Sprague 1985).

The magnitude of the increase in aluminum tolerance is similar to those reported in the literature for other metals, following pre-exposure to "medium" levels of 0.35–0.6 LC50 (1.9 times for copper and rainbow trout, Dixon and Sprague 1981b; 1.6–1.9 times for copper and coho salmon (*Oncorhynchus kisutch*), McCarter and Roch 1983, 1984; 2.5 times for zinc and rainbow trout, Bradley and Sprague 1985; 1.8 times for cadmium and white sucker (*Catostomus commersoni*), Duncan and Klaverkamp 1983; 1.7 times for cadmium and fathead minnows (*Pimephales promelas*), Benson and Birge 1985; 1.7 times for mixtures of the above metals and chinook salmon (*Oncorhynchus tshawytscha*), Roch and McCarter 1984b; and up to 1.5 times for these mixtures and rainbow trout, Roch and McCarter 1984a). Previous work on acclimation of fish to aluminum was not carried to the stage of estimating tolerance or LC50s. Guthrie and Schofield (1982) found less mortality among brook trout fry and yearlings gradually acclimated during 4–5 d to final levels of pH 5 and 200 or 400 μg Al/L than among fish suddenly exposed. These concentrations of aluminum bracket the LC50s we found for acclimated rainbow trout. Research that assessed acclimation in terms of resistance times instead of tolerance levels has been omitted from discussion.

The rapid development of increased tolerance during 7 d is similar to that found for copper and zinc in our laboratory (Dixon and Sprague 1981b; Bradley and Sprague 1985) and to speed of increase in copper tolerance of coho salmon (McCarter and Roch 1983) and cadmium tolerance of white sucker (Duncan and Klaverkamp 1983). The similarity in degree and rate of acclimation between aluminum and the other metals suggests a similar defence mechanism. The mechanism for acute lethal action of aluminum is also similar to that of other metals, with general necrosis of gills and, in some cases, mucous accumulation with likely results of anoxia and impaired ion exchange (Muniz and Leivestad 1980; Schofield and Trojnar 1980; Baker and Schofield 1982; Tandjung et al. 1982).

We found no clear evidence of a change in degree of acclimation as the pre-exposure continued, and results in the literature for other metals are in general agreement. There appeared to be a trend for copper tolerance to increase from day 7 to day 21 of pre-exposure, but changes were too slight to draw definite conclusions (Dixon and Sprague 1981b). Duncan and Klaverkamp (1983) concluded that there was no difference in cadmium tolerance between 7 and 14 d of pre-exposure. For zinc, Bradley and Sprague (1985) found pre-exposed to control ratios of 2.5 after 1 wk, 2.7 at 2 wk, and 2.3 at 3 wk, again probably chance variation. McCarter and Roch (1983) concluded that there was a steady loss of acquired tolerance during a long pre-exposure to copper, but calculations from their pairs of pre-exposed and control LC50s indicate that the loss was only about 17% from the first to the eighth week.

Other researchers have compared the effects of medium and high pre-exposure levels, with various findings. As mentioned above, copper tolerance of trout was much the same for pre-exposures of 0.4 and 0.6 LC50 (Dixon and Sprague 1981b). However, coho salmon showed apparently greater increase of copper tolerance at higher pre-exposures (about 1.6, 1.7, 1.9, and 2.2 times control values for pre-exposures of 0.38, 0.50, 0.55, and 0.75 LC50, McCarter and Roch 1983, 1984). White sucker also showed greater gain in tolerance of cadmium (2.45 times) for a high pre-exposure of 0.66 LC50 than they did (1.75 times) for a medium pre-exposure of 0.37 LC50 (Duncan and Klaverkamp 1983). It is difficult to reconcile these findings but we repeat that the ratios derived from individual LC50s could vary by chance, aside from possible species differences.

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BOOK REVIEWS / COMPTES RENDUS

Nitrogen in the marine environment. *Edited by Edward J. Carpenter and Douglas G. Capone. Academic Press Inc., New York and London. 1983. XVII and 900 p. $59.00.*

For reasons not fully understood, nitrogen rather than phosphorus is the nutrient controlling primary production over much of the oceans. As with P, the biological cycle of N in open waters involves a short circuit within the upper, sunlit layers through uptake by plants and recycling by degraders, and a long one via gravity-mediated settling of N-containing living and dead material to greater depth. In contrast with P, the cycle of N involves more than one dissolved inorganic moiety whose rates of uptake and release, however, can be routinely measured even at sea. Hence, we know much more about the rates and routes of N than P; also, the marine workers might at present be ahead of their freshwater colleagues with respect to the understanding of nutrient cycling. According to a search of the Biosis® Data Base by the editors of the book, the number of papers published per year on N in the marine and brackish domains has increased severalfold between 1970 and 1980, while that for P has not; the same divergence could not be found for the freshwater literature. In parallel, our enhanced knowledge regarding the processes in the pelagic as well as benthic realms makes a book possible now where a chapter or two sufficed two decades ago.

The editors have induced a large number of mostly biologically oriented authors to write comprehensive reviews, each with a great many citations but without attaining handbook character, that is to say, the reviews remain readable. The overall style and layout, combined with the scope and high quality of the content, should induce many to read rather than scan the book. Many chapters will be very informative also for limnologists — and not only those concerned with big, deep lakes — because so many principles regarding organisms and routes of transfer apply to aquatic habitats at large. A few chapters are suitable as assigned reading in graduate courses. I regard the book as a road mark and as the best overall source to turn to for, presumably, the next several years.

The work is divided into four sections: Distributions (including inorganic, organic, and gaseous compounds); processes (ranging from N-fixation and regeneration in the water column and on the bottom, through uptake kinetics and algal metabolism, to invertebrate nutrition and zooplankton excretion, to man's impact on the marine [biological] nitrogen cycle); systems (N in major marine domains including saltmarshes, but also symbioses [liberally defined], and macroalgae); and methods (including a brief chapter on simulation models that does not treat water quality issues). Methods are, of course, introduced in many of the topic-oriented chapters, since the evaluation of so many data (and the stands taken by the authors) depend on an understanding of the largely nonstandardized measurements. The book's emphasis on water column issues reflects the recent history of research during the roughly two decades since the introduction of N isotopes into marine work. However, three chapters specifically dealing with the bottom, and sections in a few others show the rising appreciation of the role of the seabed. (Does half or more of the denitrification in the sea take place in sediments?) Among chapters, there is little apparent redundance in coverage, although there is also no obvious integration, for instance, by systematic cross-referencing among chapters; an index, though, is provided. The restraint by (or on?) the authors to present little or none of their own research for the first time is noticeable.

It is tempting to conclude by wondering what might be very different in a treatment of the same scope, 10 yr hence: certainly heterotrophic bacteria will be given more emphasis and will not be treated largely as "black-box" degraders. Along with that will be a better appreciation of the microbial loop, including the protozoans. In parallel, our understanding of the organic dissolved N (and the particulate as well, I suppose) will have been greatly altered by high-pressure liquid chromatography by then. The relation between external, low concentrations of ammonium and nitrate and algal uptake rates will have been reworked with the new, highly sensitive analytical methods, and perhaps we will know how to find phytoplankton growth rates in terms of N in the field from measured uptakes rate (and hopefully, will not any longer normalize uptake velocities by total particulate N but use plant-N, somehow). We are likely to have in hand complete N budgets, with all major constituents measured, for some systems or domains, as well as a global geochemical N budget that balances. All the above subjects are not fully satisfactorily treated in the present book but this is where the field is at present. These shortcomings (and I am sure, there are more) are the research challenge for the future which, come to think of it, is in many respects (e.g. the new analytical methods) already with us.

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(R579)

BOOKS RECEIVED/LIVRES REÇUS

Fish aquaculture: technology and experiments. *Christoph Meske. Edited and translated by Frederick Vogt. Pergamon Press, Inc., New York, NY. 1985. 237 p. $48.00 (U.S.). ISBN 0-08-024920-5 (hardcover); $30.00 ISBN 0-08-024019-1 (flexicover).* This is an updated and enlarged version of Professor Voyt's original book published in German in 1973. The work concerns the continuous production of warmwater table fish independent of climate or other environmental concerns. The work reported refers solely to a closed cycle system. [R675]

Wetlands of the United States: current status and recent trends. *Ralph W. Tiner, Jr. U.S. Fish and Wildlife Service, Newton Corner, MA 02158. 1984. 59 p.* A report on the current status of U.S. wetlands and major areas where wetlands are in greatest jeopardy. Also included is information on wetland trends on a regional and national level. [R679]

Chemical processes in lakes. *Werner Stumm (editor). John Wiley & Sons, Inc., New York, NY. 1985. 435 p. $59.95 (U.S.). ISBN 0471-88261-5.* A multidisciplinary study of the dynamics and mechanisms of aquatic systems by natural scientists, oceanographers, limnologists, and environmental engineers. The emphasis is on explanation and intellectual stimulation rather than comprehensive documentation. The concepts presented apply to all natural water systems, including oceans, rivers, and estuaries. The contributors illustrate their conclusions on the factors that regulate the concentrations of elements and compounds with steady-state and dynamics models. [R688]

Dam design and operation to optimize fish production in impounded river basins. CIFA Technical Paper 11. *G. M. Bernacsek. Food and Agriculture Organization of the United Nations, Rome 1984. 98 p. ISBN 92-5-101485-X.* A series of guidelines are presented; these are based on a review of the ecological effects of large dams in Africa. [R689]

Fish and shellfish pathology. *Anthony E. Ellis (editor). Academic Press Inc., Publishers, Orlando, FL. 1985. 412 p. $69.50 (U.S.) £53.50. ISBN 0-12-237490-8.* The proceedings of the First International Conference of the EAFP (European Association of Fish Pathologists) held in Plymouth, England, in September 1983. The current status of diagnostics, chemotherapy, and vaccination are critically reviewed. Contributions encompass many aspects of fish and shellfish pathology. [R690]

Small-scale fisheries in Asia: socioeconomic analysis and policy. *Theodore Panayotou (editor). International Development Research Centre, Ottawa,Ont. 1985. 283 p. ISBN 0-88936-424-9.* This volume is a partial response to the need for a better understanding of the constraints and opportunities facing small-scale fisheries. [R691]

Mapping strategies in chemical oceanography. *Alberto Zirino (editor). American Chemical Society, Washington, DC. 1985. 468 p. $89.95. ISBN 0-8412-0862-X.* Based on a symposium held in Seattle, 20–25 March 1983, which focussed on current approaches to chemical and biological mapping of the oceans. The papers give a practical overview of "chemical" mapping with discussions on method development, sampling, data collection, and analysis. [R692]

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia **T. D. Beacham and C. B. Murray**

Winter survival and growth of *Chondrus crispus* in onshore culture tanks **P. F. Shacklock and J. S. Craigie**

Environmental and parental influences on age at maturity in sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia **R. M. Peterman, M. J. Bradford, and J. L. Anderson**

Effects of chronic exposure to sublethal pH on growth, egg production, and ovulation in brook trout, *Salvelinus fontinalis* **W. H. Tam and P. D. Payson**

Changes in mean weight, sea-age composition, and catch-per-unit-effort of Atlantic salmon (*Salmo salar*) angled in the Godbout River, Quebec, 1859–1983 **A. T. Bielak and G. Power**

Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca* **M. Stephenson and G. L. Mackie**

Introduction: Phosphorus–Plankton Dynamics Symposium **S. J. Tarapchak and C. Nalewajko**

Does algal–bacterial phosphorus partitioning vary among lakes? A comparative study of orthophosphate uptake and alkaline phosphatase activity in freshwater **D. J. Currie, E. Bentzen, and J. Kalff**

Phosphate uptake by microorganisms in lake water: deviations from simple Michaelis–Menten kinetics **S. J. Tarapchak and L. R. Herche**

Microbial recycling of phytoplankton phosphorus **J. V. De Pinto, T. C. Young, J. S. Bonner, and P. W. Rodgers**

Phosphorus regeneration by the predatory copepod *Diacyclops thomasi* **J. A. Bowers**

Epilimnetic phosphorus cycling: influence of humic materials and iron on coexisting major mechanisms **D. A. Francko**

Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes **C. L. Schelske, E. F. Stoermer, G. L. Fahnenstiel, and M. Haibach**

Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition **E. Sakshaug and Y. Olsen**

Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures **C. F. D'Elia, J. G. Sanders, and W. R. Boynton**

Identification of critical nutrient levels through field verification of models for phosphorus and phytoplankton growth **M. T. Auer, M. S. Kieser, and R. P. Canale**

Dissolved organic phosphorus compounds: do they satisfy planktonic phosphate demand in summer? **R. T. Heath**

A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227, northwestern Ontario **S. N. Levine, M. P. Stainton, and D. W. Schindler**

Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient **S. S. Kilham**

Light history, phosphorus status, and the occurrence of light stimulation or inhibition of phosphate uptake in Lake Superior phytoplankton and bacteria **C. Nalewajko, B. Paul, K. Lee, and H. Shear**

Synopsis: Phosphorus–Plankton Dynamics Symposium **S. J. Tarapchak and C. Nalewajko**

Zooplankton species abundance and biomass in relation to occurrence of *Mysis relicta* (Malacostraca: Mysidacea) **R. W. Nero and W. G. Sprules**

Influence of salmonid predation and weather on long-term water quality trends in Lake Michigan **D. Scavia, G. L. Fahnenstiel, M. S. Evans, D. J. Jude, and J. T. Lehman**

Limnetic zooplankton assemblages in Atlantic Canada with special reference to acidification **J. H. C. Carter, W. D. Taylor, R. Chengalath, and D. A. Scruton**

Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: a predictive approach **V. Crecco, T. Savoy, and W. Whitworth**

Reviews/Synthèses

El Niño, international variability and fisheries in the northeast Pacific Ocean **L. A. Mysak**

Notes

Possible effects of the Sitka eddy on sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) migration off southeast Alaska **K. Hamilton and L. A. Mysak**

Book reviews/Comptes rendus

The restoration of rivers and streams: theories and experience (edited by James A. Gore) **H. B. N. Hynes**

Books received/Livres reçus
Announcements/Avis
Corrections to recent publications/Corrections sur récents publications

Guide for Authors

Introduction

We welcome manuscripts reporting significant new information in fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and cover numerous disciplines including biology and ecology of marine and freshwater organisms, physiology, toxicology, genetics, limnology, oceanography, economics, disease, and management.

Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to those whose experimental results emphasize causal mechanisms underlying observed phenomena rather than pure description and fact. Manuscripts should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. Their novelty must relate to more than the particular (a certain year, place, taxon, chemical compound) and their contribution to science must clearly be beyond the confirmatory state.

Manuscripts submitted should be as comprehensive as possible; research fragments are generally unacceptable. If a single paper cannot be produced, then closely related papers should be cross-referenced and submitted together. The paper should not be submitted or accepted for publication elsewhere.

The *Journal* considers the following types of contributions:

Articles: Studies of broad scope that are original contributions to science.

Notes: Reports of significant new knowledge arising from problems with narrow limits or important findings that warrant immediate publication before broader studies are complete. Notes should occupy no more than 3 printed (9 manuscript) pages.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science of concern to the professional and layman. References are desirable; informal style is welcome.

Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

Manuscript Submission

Submit manuscripts in triplicate to the Editor, accompanied by a covering letter that (1) states the main points and significance of the work, (2) accepts the mandatory $44 page charge, (3) suggests potential referees, and (4) identifies other manuscripts containing the same or similar information. The page charge can be waived only if the work is of unusually high quality and grant support is lacking. Original typescripts and figures (except halftones) are best retained by the author until requested.

Each manuscript is normally submitted to two referees for appraisal before final evaluation by an editor. However, the Editor will return unreviewed those manuscripts that do not fall within the *Journal's* editorial policy or scope.

Editorial Practices

The *Council of Biology Editors Style Manual* (5th ed. CBE, 9650 Rockville Pike, Bethesda, MD 20814) is used as the authority in matters of form. The standards for spelling are either *Webster's Third International Dictionary* or the *Oxford English Dictionary* and *Le Grand Larousse encyclopédique*. Authors are responsible for consistency in spelling. Titles of periodicals are abbreviated as in *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103). Authors are responsible for ensuring the accuracy and completeness of their reference list. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (4th ed. 1980), Spec. Publ. No. 12, American Fisheries Society. All measurements must be metric, use SI symbols in most instances (exceptions noted in editorial in the *Journal*, Vol. 40, No. 12), and adhere to the *Canadian Metric Practice Guide* CAN3-Z234.1-79 (Canadian Standards Association, 178 Rexdale Boulevard, Rexdale, Ont. M9W 1R3).

Series titles should be avoided. An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty reprints are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs).

Preparation of Manuscripts

General Guidelines

Movement of manuscripts through review channels and the editorial office is greatly expedited if manuscripts are prepared in *Journal* style and format. When in doubt about specific details, consult a current issue of the *Journal*. General guidelines follow.

Type the manuscript on white paper, preferably 21.5×28 cm (8.5 × 11 in.), on only one side of the page. If possible, use paper with lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations.

Double-space all parts of the manuscript, including tables, captions for tables and figures, footnotes, and the reference list. Underline only material that is to be printed in italics.

Do not use all capitals anywhere in the manuscript.

Use the name-and-year system for literature citations.

Checklist for Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data repository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the *results* supported by the data provided? Are findings distinguished from inferences? Is the *discussion* limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

1) Insert bibliographic strip before the abstract (Authors, date, title, Can. J. Fish. Aquat. Sci.).

2) Limit abstract to one paragraph of about 175 words.

3) Double-space all elements of the manuscript, including references, table captions, and figure legends.

4) Avoid exclusive use of capitals everywhere in the manuscript, including headings, table captions, and figure legends.

5) Underline only Latin names of organisms and certain statistical and mathematical notation to indicate italics.

6) Use correct SI symbols for units of measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.

7) Avoid ambiguous forms such as g $C/m^2/d$; use g $C\cdot m^{-2}\cdot d^{-1}$.

8) Identify test used to test statistical significance and give probability value. No reference is needed for common statistical tests.

9) In the text, generalize from tables and figures; avoid repeating all the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

10) Include acknowledgments section at manuscript stage, not when galley proofs arrive.

11) Provide the person's initials and mailing address when referring to personal communications.

12) Delete unnecessary references that do not apply directly to the problem.

13) Check references carefully against text citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g. available from Department of Economics, Simon Fraser University, Burnaby, B.C. V5A 1S6.

14) Delete commas between name and date in citations such as (Smith 1900) and do not underline "et al."

15) Replace 10^n in table headings and figure axes with appropriate SI prefixes or use words (e.g. thousands).

16) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints of figures, or originals if they do not exceed 21.5 × 28 cm, on request for publication. Use the same type of lettering throughout if possible.

Parts of the Manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximum amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g. X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to . . ." or "Investigations on . . ." Good titles greatly assist scientists and librarians in using scientific literature and aid indexers preparing titles for keyword indexes.

Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "... is discussed" or "... was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents.

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exeed 375–500 words.

Materials and Methods

Materials and Methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine ... we ..." If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and digest them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made and so avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the titles. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Empahsis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgments

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence. Nearly every manuscript submitted to the *Journal* contains errors in the references.

Tables

Tables are used to present repetitive data and should be as economical of space as possible.

Design tables to fit within either a column or page of the *Journal*.

Type each on a separate page and number with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines.

Figures

Provide photographic reproductions or the original artwork (no larger than 21.5 × 28 cm) of each illustration. If submitting photographs, type the author's name and figure name on a strip of paper and fasten to the back of the print. Do not write on the illustration itself. Provide two photocopies of line illustrations and two sets of any photographs for review purposes.

Design figures to fit a 1-, $1\frac{1}{2}$-, or 2-column width of the *Journal* and ensure that all lettering, numerals, and symbols are legible, neat, and at least 1.5 mm high when reduced. Figures should not be mounted, stapled, or clipped. When possible, figures should be grouped and be done with the same or similar type of lettering.

Type legends in succession on a separate page. Add bar scales to maps, photomicrographs, equipment diagrams, etc.

Where each figure is first referred to, type "Fig. — near here."

Computer-generated figures should be avoided if possible, as they usually reproduce poorly. Dot-matrix® printers cannot produce sufficiently dark, solid lines to ensure legibility. Figures drafted in black india ink are always preferable. If sheets of printed characters are used, be sure they adhere completely.

Draft rather than type axis labels for graphs.

Color plates are very expensive to produce and should only be used where the color being presented is essential to the understanding of the text. Extra costs for the reproduction of color plates are usually charged to the author. Submit only the most outstanding photographs for color reproduction. We prefer to use color photographs, but will accept drawings, color negatives, slides, or film positives.

Mathematical Expressions, Equations, and Formulae

Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulae. In the various expressions, place each component in its correct position.

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the number *one*, and between the capital *O* and the numeral *zero*. Make other explanatory notes similarly.

Appendix

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel	Bq
calorie	cal
centimetre	cm
centimetre, square	cm^2
centimetre, cubic	cm^3
centimetre per gram per second	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
day	d
decimetre	dm
degree Celsius	°C
degrees of freedom	df
gram	g
hectare	ha
hertz	Hz
hour	h
joule	J
kilometre	km
litre	L
lumen	lm
lux	lx
metre	m
metre, square	m^2
metre, cubic	m^3
micrometre	μm
milligram	mg
millilitre	mL
millimetre	mm
millimetre, square	mm^2
minute	min
molar mass	*M*
mole	mol
month	mo
Pascal	Pa
second	s
standard deviation	SD
standard error	SE
tonne	t
volt	V
volume	vol
watt	W
week	wk
year	yr

Dates

Dates may be written in the sequence day-month-year without internal punctuation (On 9 October 1983 the . . .), or the alternative sequence month-day-year may be employed with the year set off by commas before and after it (On October 9, 1983, the . . .).

Reference Citations in Text

Name-and-year system

The *Journal* uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared . . ." or ". . . were compared (Brown 1983)." If the reference has more than two authors, include only the surname of the first author followed by "et al." (not italicized): "Brown et al. (1983) compared . . ." or ". . . were compared (Brown et al. 1983)."

Personal communications

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "pers. comm."

Unpublished data

If the unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "(In press)." Only those manuscripts that are in galley or page proof or for which there is an acceptance letter can be considered in press. If the article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpubl. data" in the text and do not include it in the reference list.

Reference Lists

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *Serial Sources for the BIOSIS Data Base*) for references.

Journal article

Peterman, R. M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444–1452.

Entire issue of journal

Gordon, D. C. Jr., and A. S. Hourston [ed.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40(Suppl. 1): 1–365.

Book in a series

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Book not in a series

LeBlond, P. H., and L. A. Mysak. 1978. Waves in the ocean. Elsevier, New York, NY. 602 p.

Part of book

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia, p. 203–229. *In* W. J. Neil and D. C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

Corporate author

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

Theses

KUTTY, M. N. 1966. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 102 p. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

SMITH, J. E. 1981. Catch and effort statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1032: 90 p.

Translation

KOIKE, A., AND M. OGURA. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983)

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h," "min," and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Word List

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the *Journal's* house style for these commonly used terms:

- age-class (n.)
- age-group (n.)
- aquaculture (n.)
- Arctic char (n.)
- brackish water (n.)
- brackish-water (adj.)
- chi-square (n., adj.)
- cold water (n.)
- cold-water (adj.)
- deep sea (n.)
- deep-sea (adj.)
- deep water (n.)
- deepwater (adj.)
- freshwater (n., adj.)
- fresh water (n.)
- groundwater (n., adj.)
- hard water (n.)
- hardwater (adj.)
- headwater (n., adj.)
- lake water (n., adj.)
- meltwater (n., adj.)
- open water (n.)
- open-water (adj.)
- percent (n.)
- salt water (n.)
- saltwater (adj.)
- sea-run (adj.)
- seawater (n., adj.)
- shallow water (n.)
- shallow-water (adj.)
- short term (n.)
- size-class (n.)
- snowmelt (n.)
- soft water (n.)
- softwater (adj.)
- tidewater (n., adj.)
- *t*-test (n., adj.)
- warm water (n.)
- warmwater (adj.)
- year-class (n.)
- young-of-the-year (n., adj.)

Guide des auteurs

Introduction

Les manuscrits comportant une information nouvelle dans le domaine des sciences halieutiques et aquatiques sont les bienvenus. Ils peuvent se rapporter aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatiques, et couvrir de nombreuses disciplines, y compris biologie et écologie des organismes marins et dulçaquicoles, physiologie, toxicologie, génétique, limnologie, océanographie, économique, maladies et gestion.

Les critères de sélection des manuscrits dépendent de l'étendue et de l'importance des connaissances ou idées nouvelles qu'ils contiennent. On donnera la préférence à ceux dont les résultats expérimentaux font ressortir les mécanismes sous-jacents aux phénomènes observés plutôt qu'une simple description ou énoncé de fait. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles en faisant plus que corroborer des faits.

Les manuscrits soumis devraient être aussi complets que possible ; des fragments de recherche sont généralement inacceptables. S'il est impossible de produire un seul article, on devra soumettre ensemble des articles étroitement liés entre eux, avec références croisées. L'article ne doit pas avoir été soumis ou accepté pour publication ailleurs.

Le *Journal* considère les types de contributions suivants :

Articles : études d'une portée générale, constituant des contributions inédites à la science.

Notes : communications brèves signalant une connaissance nouvelle et significative découlant de problèmes étroitement limités et facilement définis, ou d'importantes découvertes qui méritent d'être publiées avant que des études plus vastes soient terminées. Les notes ne doivent pas dépasser 3 pages imprimées (9 pages de manuscrit).

Critiques : appréciations critiques détaillées de vastes champs de recherche, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives : essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Commentaires : opinions sur des sujets récemment exposés dans le *Journal*, et, de préférence, ne dépassant pas 500 mots.

Soumission des manuscrits

Les manuscrits doivent être soumis au rédacteur en triplicata, et accompagnés d'une lettre mentionnant : (1) les principaux points et l'importance du travail, (2) l'acceptation des frais de publication obligatoires de 44 $ par page, (3) des suggestions quant aux arbitres éventuels et (4) une mention d'autres manuscrits contenant une information identique ou qui se rapproche de celle contenue dans le manuscrit soumis. Les frais de publication pourront ne pas être débités aux auteurs qui n'ont pas reçu de subventions et dont le travail est d'une qualité exceptionnelle. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les simili) jusqu'à ce qu'on les lui demande.

Un manuscrit est normalement soumis à deux arbitres pour évaluation, avant l'évaluation finale par un rédacteur. Cependant, les manuscrits qui ne répondent pas à la politique éditoriale ou à la portée du *Journal* sont retournés à l'auteur sans avoir été soumis à l'arbitrage.

Dispositions générales

Le *Council of Biology Editors Style Manual* (5e éd., CBE, 9650 Rockville Pike, Bethesda, MD 20814) sert de guide quant à la forme de la présentation. Le *Webster's Third International Dictionary* ou l'*Oxford English Dictionary*, et le *Grand Larousse encyclopédique* font autorité pour l'orthographe des mots. L'uniformité de cette dernière est la responsabilité des auteurs. Les titres de périodiques sont abrégés suivant les *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103. C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (4e éd. 1980), Spec. Publ. No. 12, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique et, dans la plupart des cas, être exprimées en unités SI (sauf exceptions mentionnées dans un éditorial du *Journal*, vol. 40, n° 12), et se conformer au *Guide canadien de familiarisation au système métrique* CAN3-Z234.1-79 (l'Association canadienne de normalisation, 178, boul. Rexdale, Rexdale (Ont.) M9W 1R3).

On devra éviter les titres en séries. Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé.

L'auteur doit revoir les épreuves qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de modifier le contenu du texte.*

Cinquante tirés à part sont fournis gratuitement. Des tirés à part supplémentaires peuvent être achetés au moment de la publication (un bon de commande à cet affet accompagne les épreuves).

Préparation des manuscrits

Directives générales

La marche des manuscrits à travers les diverses étapes de l'arbitrage et de la révision sera grandement facilitée si les articles sont préparés dans le style et le format du *Journal*. En cas de doute sur des points particuliers, veuillez consulter une livraison récente du *Journal*. On trouvera ci-dessous des directives générales.

Dactylographiez le manuscrit sur papier blanc, mesurant de préférence 21,5 sur 28 cm (8,5 sur 11 pouces), sur un côté de la page. Si possible, employez un papier avec lignes numérotées en marge. Laissez toujours une marge d'au moins 2,5 cm.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique.

En aucun endroit du manuscrit n'écrivez entièrement en majuscules.

Pour les références citées dans le texte, utilisez le système nom et année.

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude ?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons ? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte ? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données ?

Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche ? Dans des énoncés de probabilité, seuls les tests statistiques sont-ils cités, et les tableaux statistiques inutiles sont-ils exclus ?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie ? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité ? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction ?

Le *titre* est-il représentatif du contenu du rapport ? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles ? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude ? La revue de la littérature se limite-t-elle à la définition du problème ? La section *matériel et méthodes* contient-elle le minimum de détail qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données ? Les généralisations sur les *résultats* sont-elles adéquates ? Permettent-elles de distinguer entre constatations et déductions ? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes ?

Sont énumérés ci-dessous des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

1) Insérez la bande bibliographique avant le résumé (auteurs, data, titre, Can. J. Fish. Aquat. Sci.)

2) Limitez le résumé à un paragraphe d'environ 175 mots.

3) Dactylographiez à double interligne tous les éléments du manuscrit, y compris les références et les légendes des tableaux et des figures.

4) Évitez partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.

5) Ne soulignez que les noms latins d'organismes et certaines notations statistiques et mathématiques, qui devront être imprimés en italique.

6) Dans les figures, les tableaux et le texte, exprimez les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placez un zéro avant la virgule décimale.

7) Évitez les formes ambiguës, telles que g $C/m^2/d$; utilisez plutôt g $C \cdot m^{-2} \cdot d^{-1}$.

8) Identifiez le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

9) Dans le texte, généralisez à partir des tableaux et des figures ; évitez une répétition de tous les détails. Assurez-vous que chaque tableau et figure sont indépendants et que, dans le texte, on y réfère dans l'ordre numérique. Les legendes doivent indiquer le but du tableau on de la figure.

10) Préparez la section des remerciements au stade du manuscrit et non quand vous parviennent les épreuves.

11) En référant à des communications personnelles, donnez les initiales et l'adresse postale de la personne en cause.

12) Éliminez toutes références inutiles qui ne s'appliquent pas directement au problème.

13) Vérifiez soigneusement les références en regard des citations dans le texte et vice versa, afin de vous assurer qu'il y a correspondance. Dans le cas de matériel difficilement accessible, indiquez l'endroit où le trouver, p. ex., disponible auprès du Département de l'économique, Université Simon Fraser, Burnaby (C.-B.) V5A 1S6.

14) Éliminez les virgules entre le nom et la date dans les citations telles que (Smith 1900) et soulignez *et al.*

15) Dans les en-têtes de tableaux et les axes des figures, remplacez 10^n par les préfixes SI appropriés ou utilisez des mots en clair (p. ex. milliers).

16) Aux fins de la révision, les photocopies des figures, sauf les similis, sont appropriées. Sur demende, lorsqu'il s'agira de publier l'article, envoyez des photographies des figures, ou encore les originaux, s'ils ne dépassent pas 21,5 sur 28 cm. Utilisez autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organisez le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dressez une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retouchez-les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique ; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si vous décrivez méthodes, résultats et discussion dans des sections séparées.

Organisez les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. Assurez-vous que ces derniers sont aussi clairs que possible sans référence au texte.

Commencez les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si vous donnez d'abord une conclusion que vous appuyez ensuite, non seulement votre travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voyez à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composez la phrase-thème de chaque paragraphe et disposez ces phrases dans l'ordre approprié.

Titre

Limitez le titre à ce que le travail veut démontrer. C'est la clé de l'article, et il devrait montrer clairement et de façon concise ce qui est contenu dans le travail lui-même. Le titre a deux fonctions : (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance possible de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex. rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à ... » ou « Recherches sur ... ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires.

Résumé

Le résumé doit refléter succintement le contenu et les points principaux de l'article en 175 mots environ. Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquex au début du résumé la principale conclusion de l'étude et appuyez-la par des découvertes pertinentes. Ne donnez que les détails des méthodes nécessaires à la comprehension de ce qui a été fait et insérez-les dans l'énoncé des découvertes. Évitez l'emploi de phrases telles que « ... on y analyse » ou « ... a été trouvé » ; soyez spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, et que est c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir, il est important que le résumé reflète précisément le contenu du travail.

Introduction

Limitez l'introduction à la portée, au but et à la raison de l'étude. Ne mentionnez que les travaux publiés et autre informations nécessaires à la définition du problème et à la perspective du travail. Commencez avec le but ou la portée du travail, définissez ensuite le problème et ajoutez ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375−500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limitez les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si vous présentez, autant que possible, toute l'information dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référez à ces publications et ne décrivez en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phase qui en indique le but, comme : «Afin de déterminer ... nous ...» Si la section est longue, songez à utiliser des sous-titres correspondant à ceux que vous utilisez dans la section des résultats.

Résultats

Limitez les résultats aux réponses apportées aux questions en rapport avec le but de l'étude ; que ces réponses soient aussi complètes que possibles, tout en étant concises. Exprimez ce que vous avez trouvé, autant que possible dans les mêmes termes que ceux dans lesquels les observations ou les mesures ont été faites, évitant ainsi de confondre faits et spéculations. En dégageant les généralités des tableaux et des figures, référez-y et évitez de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries des rapports ou dans un dépôt de données reconnu, et on y référera dans le texte.

Discussion

Limitez la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synethèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, notez-les et faites ressortir la manière dont vos résultats corroborent ou contredisent les travaux déjà publiés. Limitez la spéculation à ce que vous pouvez appuyer sur des preuves raisonnables. Terminez cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Évitez de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux at communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (les adresses incluant). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'encroit où l'on peut se les procurer. On doit s'assurer que les références mentionnées dans le texte correspondre à celles qui sont contenues dans la liste de références et vice versa. Presque tous les manuscrits soumis au *Journal* contiennent des erreurs dans cette section.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible.

Agencez les tableaux de façon qu'ils s'adaptent soit à une ou deux colonnes du *Journal*.

Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes.

Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplementaires.

Chaque tableau doit avoir une légende instructive, complète et indépendante.

Les renvois des tableaux doivent être indiqués par des petites lettres suscrites dactylographiées au bas du tableau.

Placez les tableaux après la liste des références.

Quand on réfère à un tableau pour la première fois, on indique dans la marge du manuscrit « Tableau — près d'ici ».

Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Figures

Fournissez des photographies ou les dessins originaux (pourvu qu'ils ne dépassent pas 21,5 sur 28 cm) de chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas sur l'illustration même. Transmettez deux photocopies des dessins au trait et deux séries de photos qui serviront au moment de la révision.

Les dessins devront occuper une largeur de 1, $1\frac{1}{2}$ ou 2 colonnes du *Journal*. Assurez-vous que tous les chiffres, lettres et symboles sont lisibles, clairs et mesurent au moins 1,5 mm de hauteur une fois réduits. Les figures ne devraient pas être montées, brochées ou fixées à l'aide de trombones. Autant que possible, elle devraient être groupées et préparées avec le même type de lettrage.

Dactylographiez les légendes, dans l'ordre, sur des feuilles séparées. Dans le cas de cartes, photomicrographies, diagrammes d'instruments, etc., ajoutez une échelle.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig.—près, d'ici ».

On devra autant que possible éviter les illustrations préparées par ordinateur, qui ne se reproduisent pas très bien. Les imprimantes par points ne peuvent produire de lignes solides suffisamment foncées pour être lisibles. On obtiendra toujours de meilleurs résultats en utilisant de l'encre de Chine noire. Si vous utilisez du lettrase instantané, veillez à ce qu'il adhère parfaitement.

Il vaut mieux dessiner que dactylographier les inscriptions relatives aux axes.

La production de planches en couleurs est très dispendieuse et on ne devrait utiliser celles-ci que lorsque les couleurs sont essentielles à la compréhension du texte. Les coûts supplémentaires de reproduction de planches en couleurs sont ordinairement débités à l'auteur. Pour les reproductions en couleurs, ne soumettez que des photos d'excellente qualité. Nous préférons utiliser des photographies en couleur, mais acceptons dessins, négatifs, diapositives ou positifs de films en couleurs.

Expressions, équations et formules mathématiques

Laissez trois espaces au-dessus et au-dessous des lignes portant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous des équations et des formules. Placez chaque composante des différentes expressions dans la position qui lui est propre.

Indiquez clairement tous les symboles. Épelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la letter *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Abréviations

N'abrégez les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

an	an
année	a
becquerel	Bq
calorie	cal
centimètre	cm
centimètre carré	cm^2
centimètre cube	cm^3
centimètre par gamme par seconde	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
décimètre	cm
degré Celsius	°C
degrés de liberté	dl
écart type	EcT
élecronvolt	eV
erreur type	ErT
farad	F
gramme	g
hectare	ha
hertz	Hz
heure	h
joule	J
jour	d
kilomètre	km
litre	L
lumen	lm
lux	lx
mètre	m
mètre carré	m^2
mètre cube	m^3
micromètre	µm
milligramme	mg
millilitre	mL
millimètre	mm
millimètre carré	mm^2
minute	min
mois	mo
masse molaire	*M*
mole	mol
pascal	Pa
seconde	s
semaine	sem
tonne	t
volt	V
volume	vol
watt	W

Dates

On écrira les dates dans l'ordre jour—mois—année, p.ex. 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le *Journal* utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : « Brown (1983) compare . . . » ou « . . . on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « *et al.* » : « Brown *et al.* (1983) comparent . . . » ou « . . . on a comparé (Brown *et al.* 1983) ».

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Article du journal

ARCHAMBAULT, D ET E. BOURGET. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. Can. J. Fish. Aquat. Sci. 40: 1278–1292.

Numéro complet du journal

GORDON, D. C., JR. ET A. S. HOURSTON [ÉD.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40 : (Suppl. 1) : 1–365.

Livre dans une série

HILTON, J. W. ET S. J. SLINGER. 1981. Nutrition et alimentation de la truite arc-en-ciel. Publ. spéc. can. sci. halieut. aquat. 55 : 17 p.

Livre ne faisant pas partie d'une série

FORRESTER, W. D. 1983. Manuel canadien des marées. Ministère des Pêches et des Océans, Service hydrographique du Canada, Ottawa (Ont.). 148 p.

Partie d'un livre

AUBERT, M., J. AUBERT, S. DANIEL ET N. DESIROTTE. 1972. État actuel de la pollution bactérienne au large des côtes françaises, p. 36–40. *Dans* M. Ruivo [éd.] La pollution des mers et les ressources biologiques. Fishing News (Books) Ltd., Londres.

Corporation-auteur

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION ET WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14^{e} éd. Washington, DC. 1193 p.

Thèse

DELISLE, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse doctorale, Univ. Ottawa, Ottawa (Ont.). 161 p.

Rapports

DUTIL, J. D., M. FORTIN ET Y. VIGNEAULT. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. manus. can. halieut. aquat 1653 : 29 p.

Traduction

KOIKE, A. ET M. OGURA. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64 : 1–11. (Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983)

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